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ASPECTS OF SPRUCE GROUSE BEHAVIOUR DURING THE BROOD PERIOD, FALL AND SPRING PHASES OF DISPERSAL, AND MIGRATION

by

Michael A. Schroeder

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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ABSTRACT

The behavioural ontogeny of spruce grouse (*Dendragapus canadensis*) was examined in a lodgepole pine (*Pinus contorta*) forest in southwestern Alberta. Particular attention was given to their behaviour during the brood period, the fall and spring phases of dispersal, and migration.

Research on 30 radio-tracked broods between 1982 and 1984 suggested that brood hens respond immediately to the sreep, sury, seer, and purring calls of juveniles. Additionally, brood hens appear to respond readily to the chicks of other broods. Brooding sessions decreased in frequency, but not duration (median of 11 minutes), until they disappeared from the behavioural repertoire of chicks at about 50 days of age. Gradually increasing hen-chick and intersibling distances, and a lack of frequent aggressive interactions among the members of a brood at the time of brood break-up, suggest that the break-up results from a decrease in the cohesiveness of the brood.

Examination of the fall phase of dispersal for 41 female and 88 male juvenile spruce grouse, analyzed for data collected between 1965 and 1984, revealed that females moved farther than males. Reasons for this difference were sought in location of wintering areas, timing of brood break-up relative to that of brood hen migration, and distance moved by migrating brood hen. Wintering areas, encompassing blocks of forest within which more than 80% of adults passed the winter, represented less than 15% of the study area. These areas were apparently also the destination for a high proportion (84%) of the juveniles. Distances moved are believed to be influenced by the location of the wintering areas in relation to the direction taken by juveniles after brood break-up occurs, as well as the timing of this event in relation to the timing of migration in adult hens. Brood break-up for juvenile males preceded that of females (4 September and 15 September, respectively), and dates of brood hen migration overlapped those of brood break-up (median of 13 September). Hence, significantly longer distances moved by juvenile females relative to males during the fall phase of dispersal may be caused by their later median date of brood break-up and consequently their increased probability of

moving with their migrating brood hens and bypassing nearby wintering areas. This possibility is supported by the observation of intact broods following the migratory paths of their mothers.

Movements by 93 radio-tagged spruce grouse between the ranges occupied during the winter and summer, were analyzed for differences between sex and age classes. The movement of a bird from the range occupied during its first winter to its first potential breeding area was considered to be the spring phase of dispersal. Subsequent movements between the breeding and wintering areas were classed as migratory movements. The similarity between distances moved during the spring phase of dispersal and migration within a sex, and the site fidelity of adult females to the range occupied during their first winter, lend support to the suggestion that migratory movements in spruce grouse retrace their dispersal movement during their first spring when about nine months old. Proportionally more females than males moved long-distances. Based on the migratory movements of adult females, short-distance migrants (moving < 2 km) were more variable than long-distance migrants in the timing of migratory movements. Additionally, short-distance migrants associated less with other adult females, especially other short-distance migrants, in winter flocks than did long-distance migrants. The behavioural differences may reflect the proximal causes producing each type of migration/dispersal.

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INTRODUCTION

Previous research on spruce grouse (*Dendragapus canadensis*) has examined the importance of behaviour on various aspects of their population biology such as mobility (Ellison 1973, Haas 1974, Herzog and Boag 1978, Lattner 1982), territoriality (McCourt 1969, McLachlin 1970, Ellison 1971, Anderson 1973, Herzog 1977, Herzog and Boag 1977, 1978, Nugent 1979, Nugent and Boag 1982), dispersal (Keppie 1975, Alway 1977, Alway and Boag 1979, Boag *et al.* 1979, Keppie 1979, 1980, Herzog and Keppie 1980), migration (Herzog and Keppie 1980), and recruitment (Boag *et al.* 1979, Keppie 1979, McKinnon 1983). Because spruce grouse are easy to handle, approach, and observe, they are excellent subjects for research on behaviour.

Many of the studies have examined the behaviour of spruce grouse at various intervals from their time of hatch to their recruitment into the population. The behavioural ontogeny of captive juvenile spruce grouse, while still in broods, suggests that the cohesiveness of the members of a brood gradually weakens until the time of brood break-up and the onset of dispersal (Alway 1977, Alway and Boag 1979). Dispersal, from their place of hatch to their place of breeding or attempted breeding, has been divided into discrete fall and spring phases, separated by a winter period during which relatively little movement occurs (Keppie 1975). Intraspecific aggression and innate behavioural differences may be proximal causes that could affect dispersal movements (Herzog and Boag 1977, 1978, Alway and Boag 1979, Keppie 1979, 1980). Additionally, the migratory movements of some adults between winter and summer ranges, have been suggested to be a retracing of movements made during their spring phase of dispersal (Herzog and Keppie 1980). Apart from documentation of these dispersal and migration movements (Keppie 1975, 1979, Herzog and Keppie 1980), the causes for the observed variability in these patterns of movement, such as distances moved, have not been examined. Furthermore, the only detailed study of spruce grouse chick behaviour has been restricted to birds in captivity; its applicability to wild situations is unknown.

Because the behaviour of juveniles has frequently been suggested to be important in determining the subsequent behavioural patterns of adults, my objectives were to examine the behavioural ontogeny of spruce grouse and consider the potential implications of their behavioural development on subsequent patterns of dispersal and migration. The results are presented as three papers:

1. Behaviour of spruce grouse broods in the field.
2. The fall phase of dispersal in juvenile spruce grouse.
3. Behavioural differences of female spruce grouse undertaking short and long migrations.

In the first paper, I examine the behavioural ontogeny of juvenile spruce grouse from their date of hatch to the period of brood break-up and fall phase of dispersal. Because earlier research on juvenile spruce grouse was done on captive birds, I also attempt to compare my observations to those of previous studies. The second paper examines in greater detail the importance of the timing of brood break-up on the fall phase of dispersal. In addition, the timing of brood hen migration, the distances of the brood hen's migratory movements, and the possible concentrations of wintering grouse, were also examined because of their potential to influence fall movements of juveniles. In the third paper, I re-examine the suggestion that migratory movements retrace a bird's dispersal movement during its first spring. I also compare some behavioural attributes of adult females undertaking short and long migrations.

LITERATURE CITED

ALWAY, J. H. 1977. A study of social behaviour relating to brood break-up and dispersal in Franklin's grouse under captive conditions. M.S. Thesis. Univ. of Alberta, Edmonton. 107p.

ALWAY, J. H., AND D. A. BOAG. 1979. Behaviour of captive spruce grouse at the time broods break up and juveniles disperse. Can. J. Zool. 57:1311-1317.

ANDERSON, L. J. 1973. Habitat use, behavior, territoriality, and movements of the male spruce grouse of northern Minnesota. M.S. Thesis. Univ. of Minnesota, Minneapolis. 119p.

BOAG, D. A., K. H. MCCOURT, P. W. HERZOG, AND J. H. ALWAY. 1979. Population regulation in spruce grouse: a working hypothesis. Can. J. Zool. 57:2275-2284.

ELLISON, L. N. 1971. Territoriality in Alaskan spruce grouse. Auk 88:652-664.

ELLISON, L. N. 1973. Seasonal social organization and movements of spruce grouse. Condor 74:375-385.

HAAS, G. H. 1974. Habitat selection, reproduction, and movements in female spruce grouse. Ph.D. Thesis. Univ. of Minnesota, Minneapolis. 124p.

HERZOG, P. W. 1977. Dispersion and mobility in a local population of spruce grouse. M.S. Thesis. Univ. Alberta, Edmonton. 98p.

HERZOG, P. W., AND D. A. BOAG. 1977. Seasonal changes in aggressive behavior of female spruce grouse. Can. J. Zool. 55:1734-1739.

HERZOG, P. W., AND D. A. BOAG. 1978. Dispersion and mobility in a local population of spruce grouse. J. Wildl. Manage. 42:853-865.

HERZOG, P. W., AND D. M. KEPPIE. 1980. Migration in a local population of spruce grouse. Condor 82:366-372.

KEPPIE, D. M. 1975. Dispersal, overwinter mortality, and population size of spruce grouse. Ph.D. Thesis. Univ. of Alberta, Edmonton. 113p.

KEPPIE, D. M. 1979. Dispersal, overwinter mortality, and recruitment of spruce grouse. J. Wildl. Manage. 43:717-727.

KEPPIE, D. M. 1980. Similarity of dispersal among sibling male spruce grouse. Can. J. Zool. 58:2102-2104.

LATTNER, M. T. 1982. Foods, mobility, habitat selection and density of spruce grouse. M. S. Thesis. Univ. of Toronto, Ontario 109p.

MCCOURT, K. H. 1969. Dispersion and dispersal of female and juvenile Franklin's grouse in southwestern Alberta. M.S. Thesis. Univ. of Alberta, Edmonton. 137p.

MCKINNON, D. T. 1983. Recruitment into a local population of spruce grouse. M. S. Thesis. Univ. of Alberta, Edmonton. 98p.

MCLACHLIN, R. A. 1970. The spring and summer dispersion of male Franklin's grouse in lodgepole pine forest in southwestern Alberta. M.S. Thesis. Univ. of Alberta, Edmonton. 153p.

NUGENT, D. P. 1979. A behavioral analysis of communication among Franklin's grouse during the breeding season. M.S. Thesis. Univ. of Alberta, Edmonton. 103p.

NUGENT, D. P., AND D. A. BOAG. 1982. Communication among territorial female spruce grouse. Can. J. Zool. 60:2624-2632.

PAPER 1: BEHAVIOUR OF SPRUCE GROUSE BROODS IN THE FIELD

INTRODUCTION

The spruce grouse is a widespread species of Tetraoninae found in the boreal forests of North America. Previous research has shown the importance of adult spruce grouse behaviour in understanding demographic aspects of the population (Ellison 1971, Herzog and Boag 1978, Keppie 1979, Boag *et al.* 1979, Herzog and Keppie 1980). Although the behaviour of juveniles has frequently been suggested to be important in determining their subsequent behavioural patterns as adults, examination of juvenile behaviour, especially while still in broods, has been limited to captive situations (Alway 1977, Alway and Boag 1979).

The purpose of this study was to examine under field conditions the behaviour of juvenile spruce grouse while in broods as a preliminary approach to determining the importance of their behavioural ontogeny on their subsequent dispersal and recruitment into the population. By repeated observations over time of broods of chicks, it was possible to describe the ontogeny of behaviour in the wild and compare it with behaviour recorded in captivity. Furthermore, the use of radio telemetry made it possible to find and observe at will wild and relatively undisturbed birds under a variety of conditions in both space and time.

METHODS

Spruce grouse broods were studied from 1982 to 1984 near the R. B. Miller Biological Station (50° 39' N, 114° 39' W) 27 km west of Turner Valley, Alberta. The study area consisted of about 10,000 ha of forest dominated by lodgepole pine, with scattered clumps of white spruce (*Picea glauca*), poplar (*Populus* spp.), and alpine fir (*Abies lasiocarpa*).

To assure access to broods immediately after their date of hatch, 23 females were noosed (Zwickel and Bendell 1967) and harnessed with radio transmitters before incubation began (early June). Nine females subsequently hatched broods successfully and were observed regularly after being found with the aid of radio telemetry. Radios were also attached to 21

additional brood hens found after their chicks had hatched, thus increasing the total sample size to 30 broods. Hatch dates for all broods were determined to the nearest day from estimated ages based on measured lengths of primary VII and IX on the chicks (McCourt and Keppie 1975).

Broods were observed between 0500 and 2230 hours for a total of about 300 hours. After the brood was initially located, an attempt was made to follow and observe it from a distance of 10-20 meters. Although observation sessions lasted as long as 10 hours, they were terminated if the brood was obviously disturbed by the observer's presence. A small percentage of brood hens (10%) was essentially impossible to follow without creating a disturbance. The rest apparently ignored us and appeared to behave normally, often moving to within a meter of the observer.

During each period of observation, scans (Altmann 1974) of the spatial dispersion, behaviour (Table 1), and vocalizations (Table 2) of each visible member of the brood and the hen were recorded every 8 minutes. Each scan took a maximum of 15 seconds to complete. All observed occurrences of display and aggressive behaviours and vocalizations were recorded, which excluded feeding, alert, and loafing behaviours and sreep, sury, and seer calls. In addition to the normal scans, the location of the brood was noted every 16 minutes and subsequently plotted on a map of the study area using a large grid system superimposed over air photos. Because of the non-normality of the data sets, all values of distances and times for a given age are given as medians rather than means.

RESULTS AND DISCUSSION

Brooding behaviour

The first phase in the post hatch life of the brood was characterized by the juvenile's dependence on brooding behaviour by the hen. Juveniles appeared to initiate brooding bouts by uttering sury calls. Although unrecorded by Alway (1977), these calls were apparently

Table 1. Behavioural repertoire of spruce grouse in brood situations.

	Origin of previous descriptions					
Behaviour	Lumsden 1961	MacDonald 1968	Harju 1969	Hjorth 1970	Alway 1977	Alway and Boag 1979
Feeding			Feeding		Feeding	
Brooding			Brooding		Brooding	
Loafing						
Preening						
Dust-bathing						
Flapping run					Flap-run	Flapping run
Alert			Alert		Alert	
Erect					Erect	
Aggressive		Aggressive	Aggressive		Aggressive	
Upright				Upright	Upright	
Jerky crouch					Nervous cro.	Jerky crouch
Crouching cum head-shaking	Head-jerk display	Squatting display		Cro. cum head-shak.	Cro. cum head-shak.	
Display walk cum tail-swaying	Strutting display	Tail-swishing display	Strutting display	D. walk cum tail-swaying	D. walk cum tail-swaying	
Rush cum momentary tail fanning	Tail-flick display	Tail-swishing display	Tail-flick display	Rush cum momentary tail fanning	Rush cum momentary tail fanning	

Table 2. Typical spruce grouse vocalizations given by the brood hen and chicks in brood situations.

	Origin of previous descriptions		
Vocalization	Harju 1969	Alway 1977	Nugent and Boag 1982
Sreep		Contact[1]	
Heep	Brooding[1]	Contact[1]	
Purring	Contentment[1]	Pleasure[1]	
Sury		Brooding	
Seer	Distress[1]	Distress[1]	
Cantus	Aggressive[1]	Aggressive[1]	Cantus[1]
	Alarm[2]		
Hum	Warning	Warning[1]	
Alarm		Alarm[1]	
Gull		Gull	

[1]The original description includes a sonogram.

[2]The sonogram and the behavioural context in which it was recorded suggest that this alarm call is actually part of the cantus.

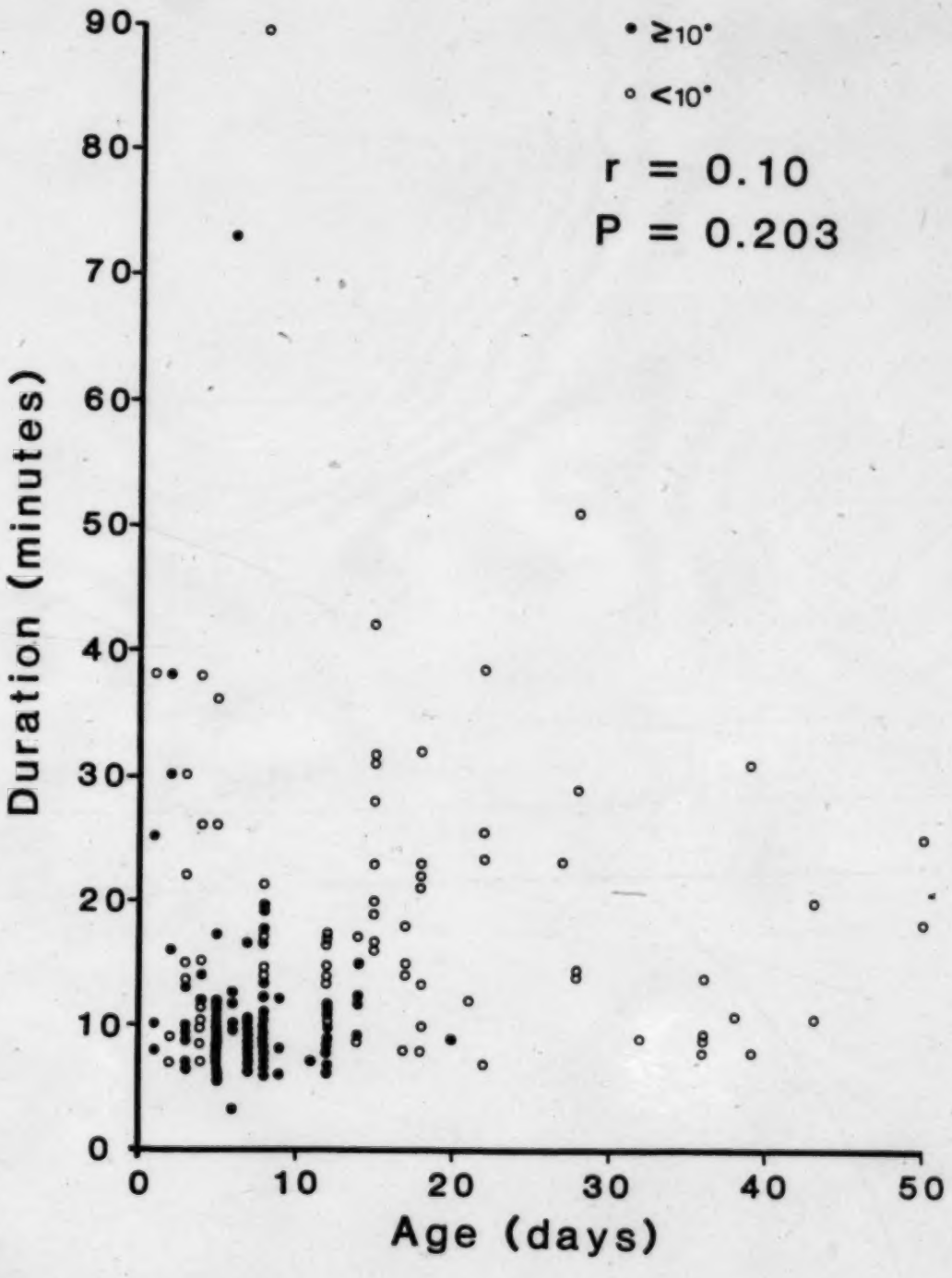
similar to sreep calls except for their slightly longer duration and ascending pitch. The similarity in the two types of calls suggests that one may be a derived form of the other. The sury call may simply be a slowed version of the sreep call. On three separate occasions, juveniles, which were being held temporarily in a darkened container in the field pending marking, gave the sury call which apparently stimulated the uncaptured hen to approach and assume a brooding posture beside the container holding the chicks.

In normal undisturbed situations, the brood hen appeared to respond to sury calls by first selecting an appropriate spot to brood her chick(s) and then assuming a brooding posture. The hen occasionally stood up and selected a second spot immediately after the initial assumption of a brooding posture. The hen typically uttered heep calls during this process. Often the chicks would follow the hen closely during this period of site selection, attempting to move under the hen while giving the sury call. After the hen selected a brooding spot and assumed a brooding posture, the chicks approached the hen from the front and pushed their way underneath (as described by Alway 1977).

Brooding bouts may have been terminated by vocal stimuli from the chicks, as chicks were frequently heard giving both sury and sreep calls while being brooded. These calls were not recorded by Alway (1977) while captive chicks were brooded, but in this study they were quite audible. Although both sury and sreep calls were uttered by chicks being brooded, sreep calls were noticeably more frequent immediately preceding the end of the brooding bout. It is possible that the hen stopped brooding the chicks when their sury calls ceased. In any case, individual chicks occasionally moved out from beneath the brood hen before she stood up, a situation very similar to that observed in wild blue grouse (*Dendragapus obscurus*)(Zwickel 1967).

The duration of brooding bouts varied around a median of 11 minutes (n = 161 undisturbed bouts), regardless of the age of the chicks (Fig. 1). Similarly, Pynnonen (1954) found that wild hazel grouse (*Bonasa bonasia*) brooded for periods of 10 to 20 minutes. In contrast, Pedersen and Steen (1979), observed brooding bouts with willow ptarmigan (*Lagopus*

Figure 1. Length of brooding bouts (n = 161) by age and temperature (°C) for spruce grouse in southwestern Alberta.

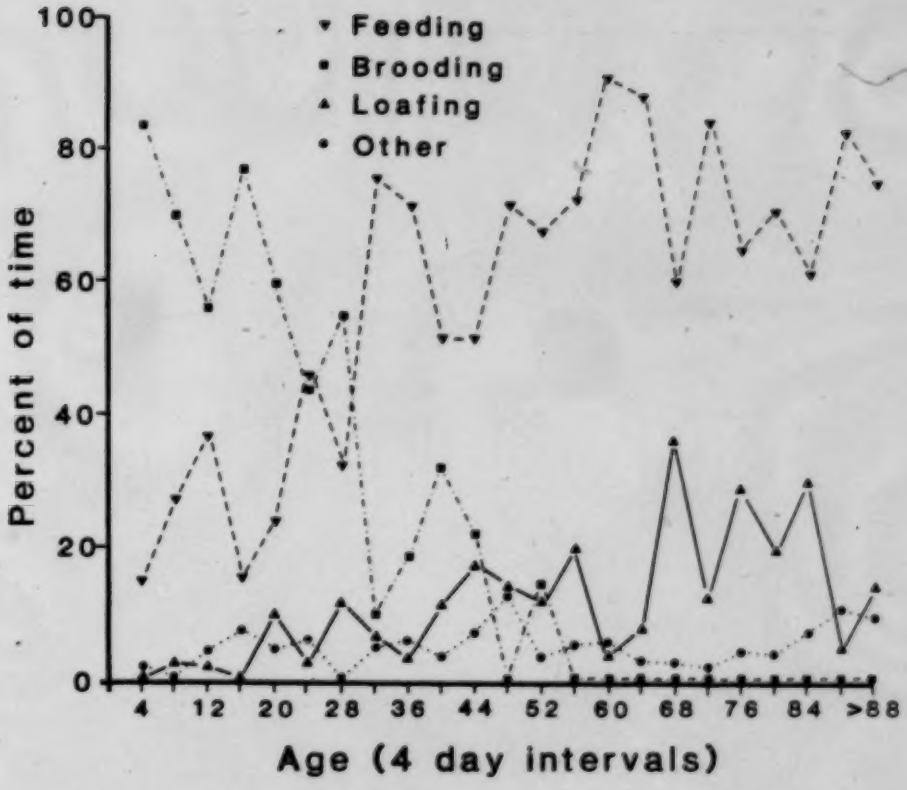


lagopus lagopus) that varied between 30 and 3 minutes and decreased with age. Although no relationship between chick age and duration of brooding bout was found in this study, more brooding bouts of old chicks (> 20 days old) than those of young chicks (< 20 days old) appeared to be in response to cool weather (< 10°C)($P < 0.001$; Chi-square contingency table).

Brooding behaviour was observed with decreasing frequency among juveniles until it disappeared from their behavioural repertoire at about 50 days of age (Fig. 2). Two extremely late brooding bouts were observed with a brood of two 50-day-old chicks. The chicks weighed approximately 280 g (as opposed to the brood hen's 450 g) and clearly displayed sexually dimorphic characteristics (one female and one male). The brood hen barely had her feet on the ground during each of the brooding bouts. One attempt at brooding resulted in the brood hen falling off the chicks as they tried to push their way underneath. Presumably a hen would be unable to brood any more than two chicks of this age because of their large size. By contrast, very early cessation of brooding was recorded in a brood of four chicks observed roosting in trees at night as early as 33 days of age.

The maximum age at which chicks were brooded in this study were compared to the 10 to 12 days of age reported for domestic fowl (*Gallus gallus*)(Wood-Gush 1955), 6 days for rock ptarmigan (*Lagopus mutus*)(Theberge and West 1973), 56 days for white-tailed ptarmigan (*Lagopus leucurus*)(Giesen, pers. comm.), 6 (Allen *et al.* 1977), 14 (Aulie 1976) or 42 (Watson and Jenkins 1964) days for willow ptarmigan (*Lagopus lagopus*), 11 days for blue grouse (Zwickel 1967), and 20 days for spruce grouse (Alway 1977). Even if the late example of brooding at 50 days in spruce grouse is not considered, brooding from 20-40 days was still relatively common (Fig. 2). Spruce grouse broods in this study differed from those in the above examples in that they typically consisted of fewer chicks (1-4) and were observed in the wild. The previously mentioned examples of brooding at 42 days by willow ptarmigan and 56 days by white-tailed ptarmigan were also observed with wild chicks. Captive spruce grouse stopped brooding at 20 days of age (Alway 1977), perhaps in response to milder conditions in

Figure 2. Activity budget by age for spruce grouse broods in southwestern Alberta.



an aviary than those apparently associated with brooding by old chicks (> 20 days old) in the wild (Fig. 1). Additionally, no broods of more than 5 chicks were observed brooding after 20 days of age. Late brooding, as observed here, may not be a necessity for chicks, but an opportunity afforded when brood sizes are small. Johnsgard (1983) suggested that ptarmigan, blue grouse, and spruce grouse might typically have smaller broods than other Tetraoninae because of the harsh climatic conditions in their nesting habitat, and thus, a constraint on the number of eggs that can be incubated. However, these results indicate that the potential necessity of brooding may be just as important as environmental constraints on the nesting period.

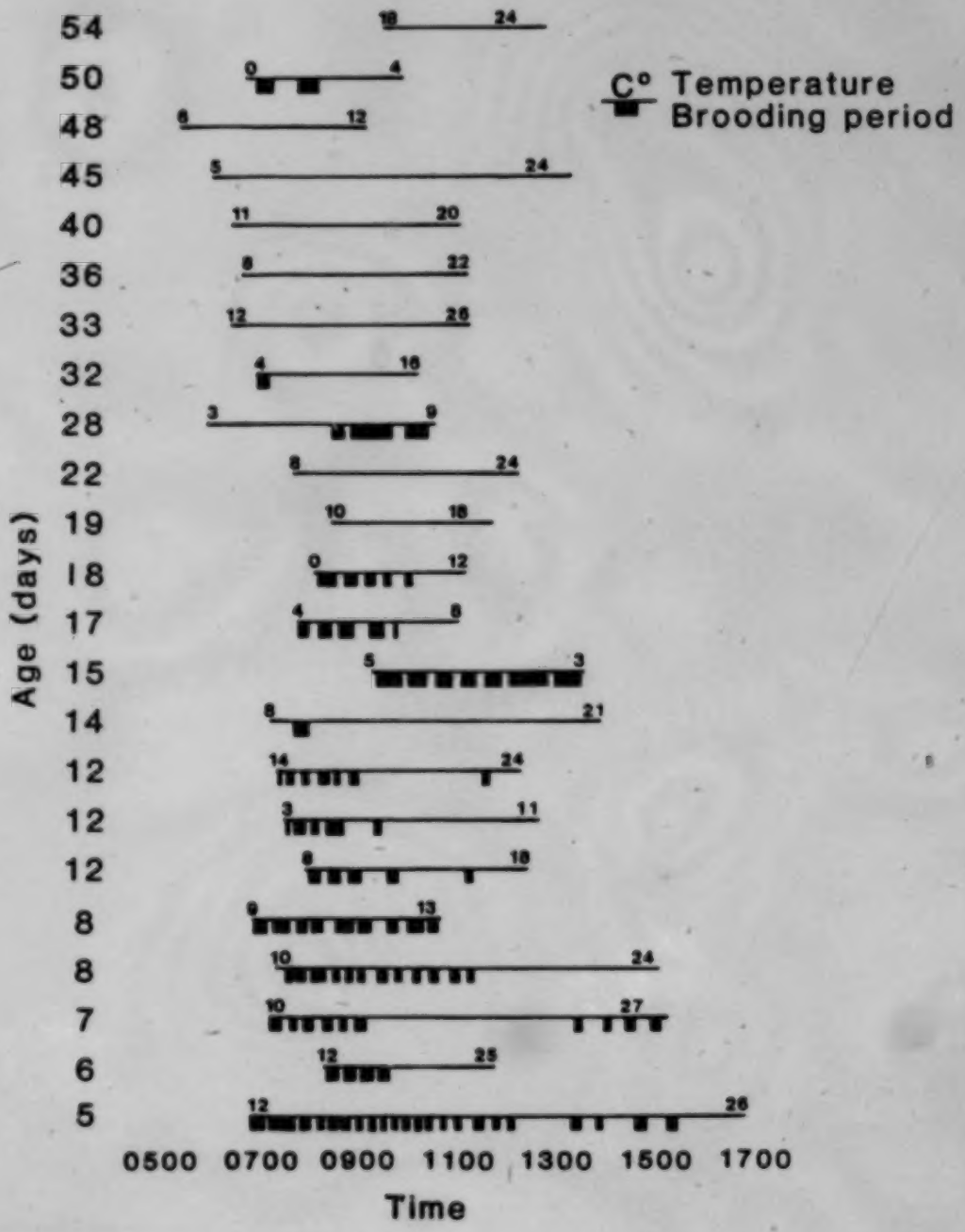
Observations of undisturbed broods over long periods of time (more than 3 hours), showed that brooding bouts tended to decrease in frequency, if not duration, during the middle of the relatively warm daylight period (Fig. 3). Notable exceptions occurred on cloudy, rainy, and/or cool days (Fig. 3; broods of 15, 17, 18, and 50 days of age). Broods observed for short periods indicated similar trends. These results suggest that brooding frequency is tied closely to both the environmental conditions and the thermoregulatory capacity of chicks, which has also been adequately shown with willow ptarmigan (Aulie 1976, Boggs *et al*. 1977, Pedersen and Steen 1979, Erikstad and Spidso 1982).

Feeding behaviour

As broods grew older and spent less time being brooded, they spent more time feeding (Fig. 2). The amount of feeding time stabilized at about 70% of the daylight hours when the chicks reached 30 days of age. The other 30% of the time was divided between brooding, loafing, and miscellaneous behaviours. As suggested by Zwickel (1967) for blue grouse, spruce grouse chicks are apparently not shown what to eat. The brood hen often fed on foods too high to be reached by the chicks.

The cohesion or contact of the feeding brood seemed to be maintained with sreep calls by the juveniles, to which the brood hen responded with heep calls. Sreep calls appeared to be

Figure 3. Brooding time in relation to the undisturbed observation time (> 3 hours) for spruce grouse broods in southwestern Alberta.



uttered in normal feeding situations when the chicks were relatively close to the hen. The sreep calls of chicks and the heep calls of hens apparently differed in both sound and function. The sreep calls of chicks were much higher in pitch than the heep calls they apparently elicited from brood hens. The difference in the two types of brood contact calls was noticeable because adult females could utter 'chick-like' sreep calls in the fall, winter, and early spring when in flocks with other spruce grouse. This was in contrast to the apparent complete cessation of sreep calls after brood break-up reported by Alway (1977), possibly because under captive conditions visual isolation was rare.

The typical dispersion patterns of feeding juveniles placed them at increasing distances from their brood hen with increasing age (Fig. 4). There was no difference between juvenile males and females ($P = 0.183$; ANCOVA). When the chicks lost contact (visual and/or auditory) with the brood hen, they gave seer calls. Seer calls typically initiated a louder heep call from the brood hen and/or a movement towards the calling chick. The distance involved when this occurred was significantly greater than during the normal feeding situation ($P < 0.001$; ANCOVA), and likewise, increased with age (Fig. 5). This was similar to the situation observed with captive spruce grouse (Alway 1977) and with wild blue grouse (Zwickel 1967). The tendency of brood hens to respond to seer calls was so strong that they would respond to seer calls of unrelated chicks and to imitations of the call by researchers.

Keppie (1977) and Alway (1977), suggested that juveniles could recognize their own brood hen. Evidence from this study supports that contention. Despite the occasional mixing of broods, young chicks in this study were never recorded abandoning their live brood hen for another. On one occasion, the seer calls of chicks in one brood, the hen of which had just died, apparently attracted another brood hen. However, the chicks of the dead hen did not follow the new hen until after about an hour had passed from the time that their own parent had died. This suggests that not only can chicks recognize their mother, but also that hens may respond to calling by orphaned chicks which they readily adopt (Keppie 1977).

Figure 4. Median distances between brood hens and feeding spruce grouse chicks at various ages in southwestern Alberta.

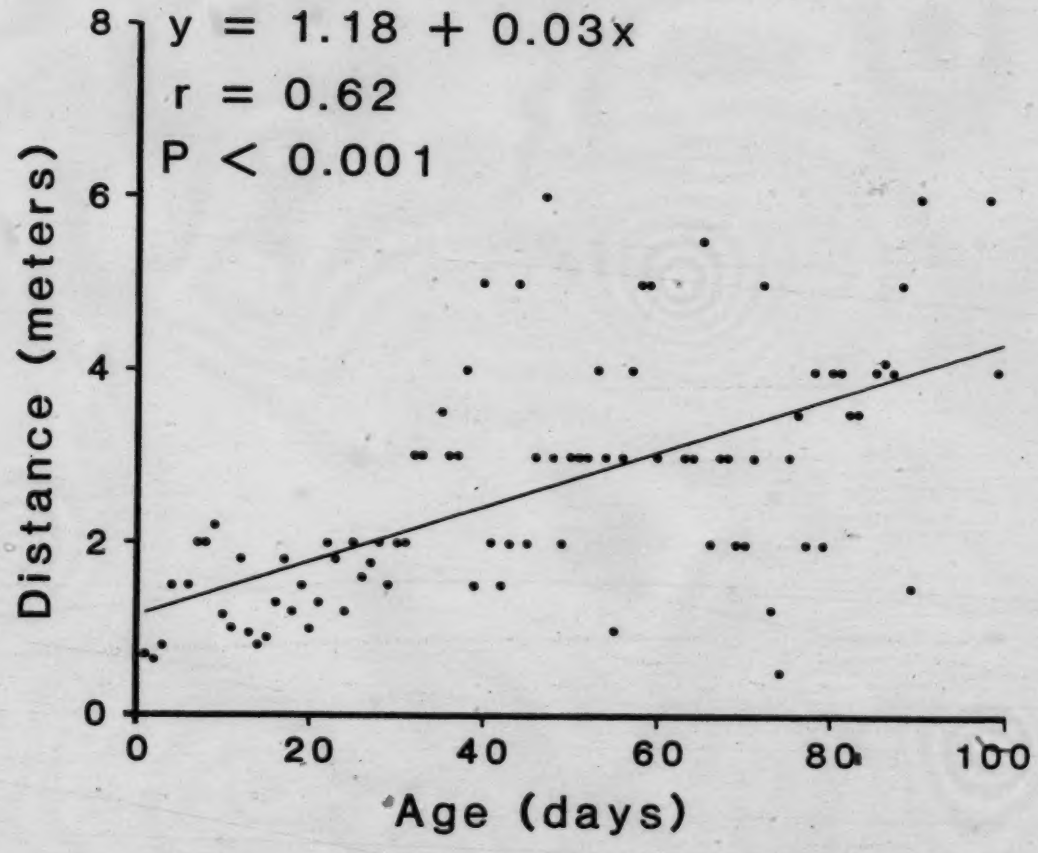
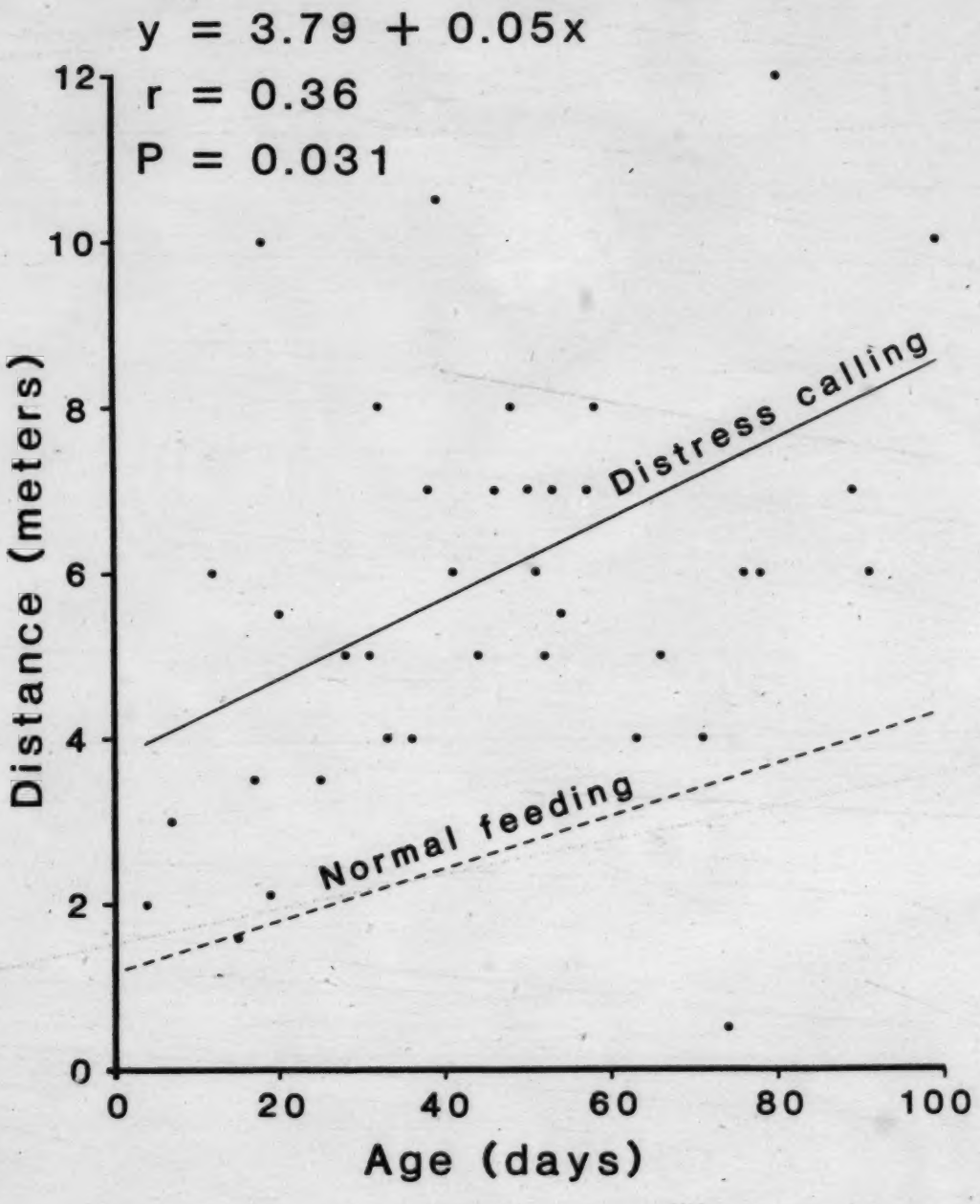


Figure 5. Median distances between brood hens and seer-calling spruce grouse chicks at various ages in southwestern Alberta (normal feeding line taken from Fig. 4 for comparison).



With increasing distances between brood hen and chicks, distances between nearest siblings also increased (Fig. 6). Bowman and Robel (1977) attributed increased intersibling distances in broods of greater prairie chickens (*Tympanuchus cupido*) to increased aggressiveness at the time of brood break-up. Observations of spruce grouse suggest that intersibling and hen-chick distances are gradually increasing throughout the brood period. The larger distances are unlikely a response to increasing intersibling or hen-chick aggression, neither of which were observed in the field. If this type of aggression occurs, it must be relatively covert. These observations support the suggestions of Alway and Boag (1979) that interindividual distances gradually increase throughout the brood period without a corresponding increase in aggressive interactions. Gradually weakening bonds that hold the brood together and/or an increasing physical ability of the juveniles to move around, more adequately explain the increased interindividual distances.

Movements initiated by the brood hen and followed by the brood appeared to be quite variable in both direction and distance (Fig. 7A, 7B, 7C). Brood hens rarely stayed in the same place for more than a few minutes when they were not brooding. When brooding bouts were eliminated from the analysis, a strong positive relationship between the age of the juveniles and the distance moved while feeding was apparent (Fig. 8). Typical movements appeared to be concentrated at the edges of meadows and in areas with a sparse canopy, which was similar to the conclusion of McCourt (1969) who found that the canopy cover at locations where broods were sighted was less than at random sites in the forest. Broods often traversed areas of dense cover with little understory, but they appeared to do so more rapidly than in other situations.

The purring call was frequently uttered by feeding chicks. It was usually given in open habitats by a chick that was actively feeding on an item that appeared to be a preferred food. In one case a juvenile feeding on a mushroom (Basidiomycetes) gave purring calls that apparently attracted its siblings, as well as its brood hen, to the same mushroom where they all fed simultaneously. Although this call appeared to attract other chicks (Alway 1977), it may

Figure 6. Median distances between sibling spruce grouse chicks at various ages in southwestern Alberta.

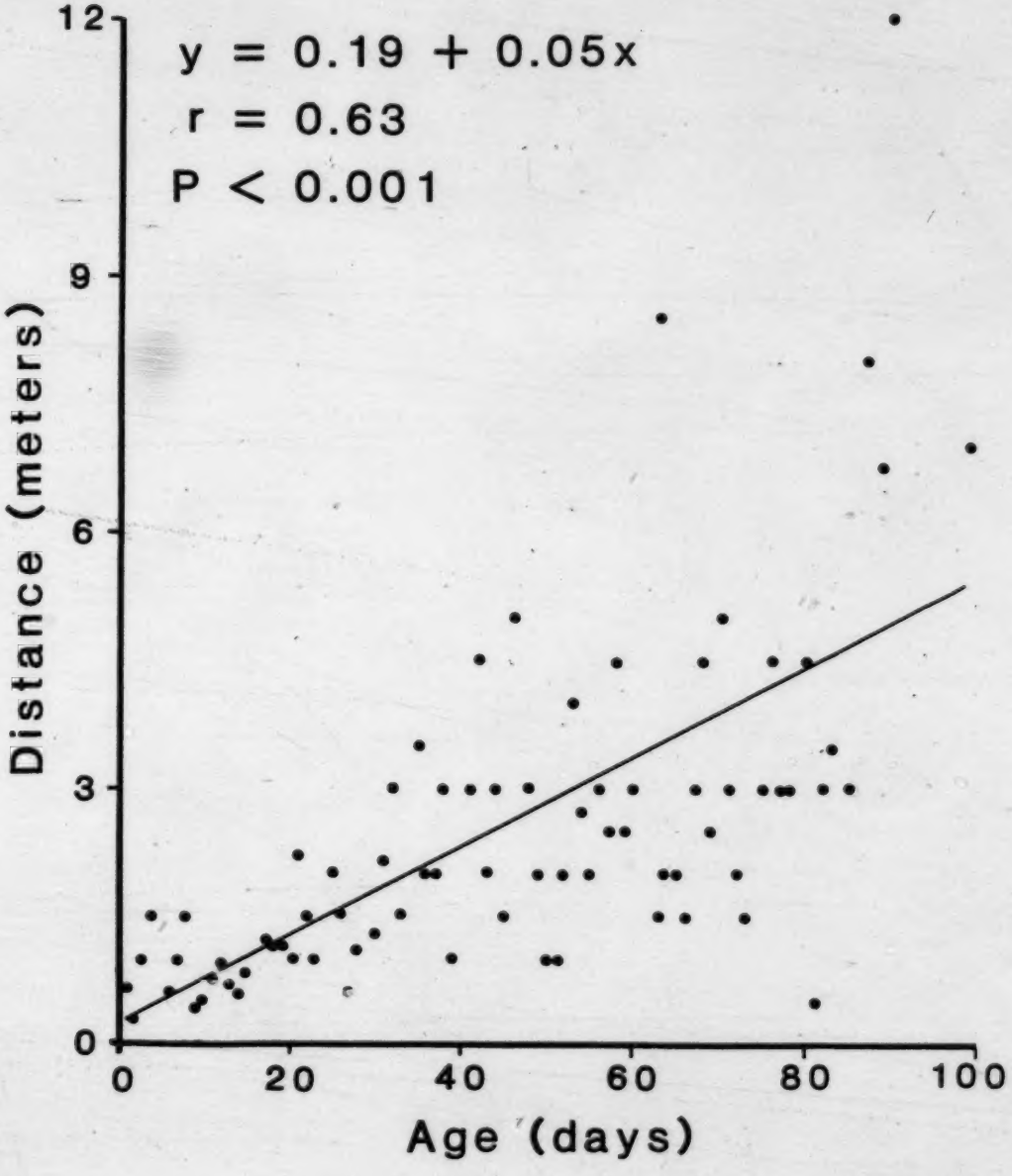


Figure 7A. Patterns of movement for spruce grouse broods observed for > 3 hours in southwestern Alberta (6 - 12 days of age).

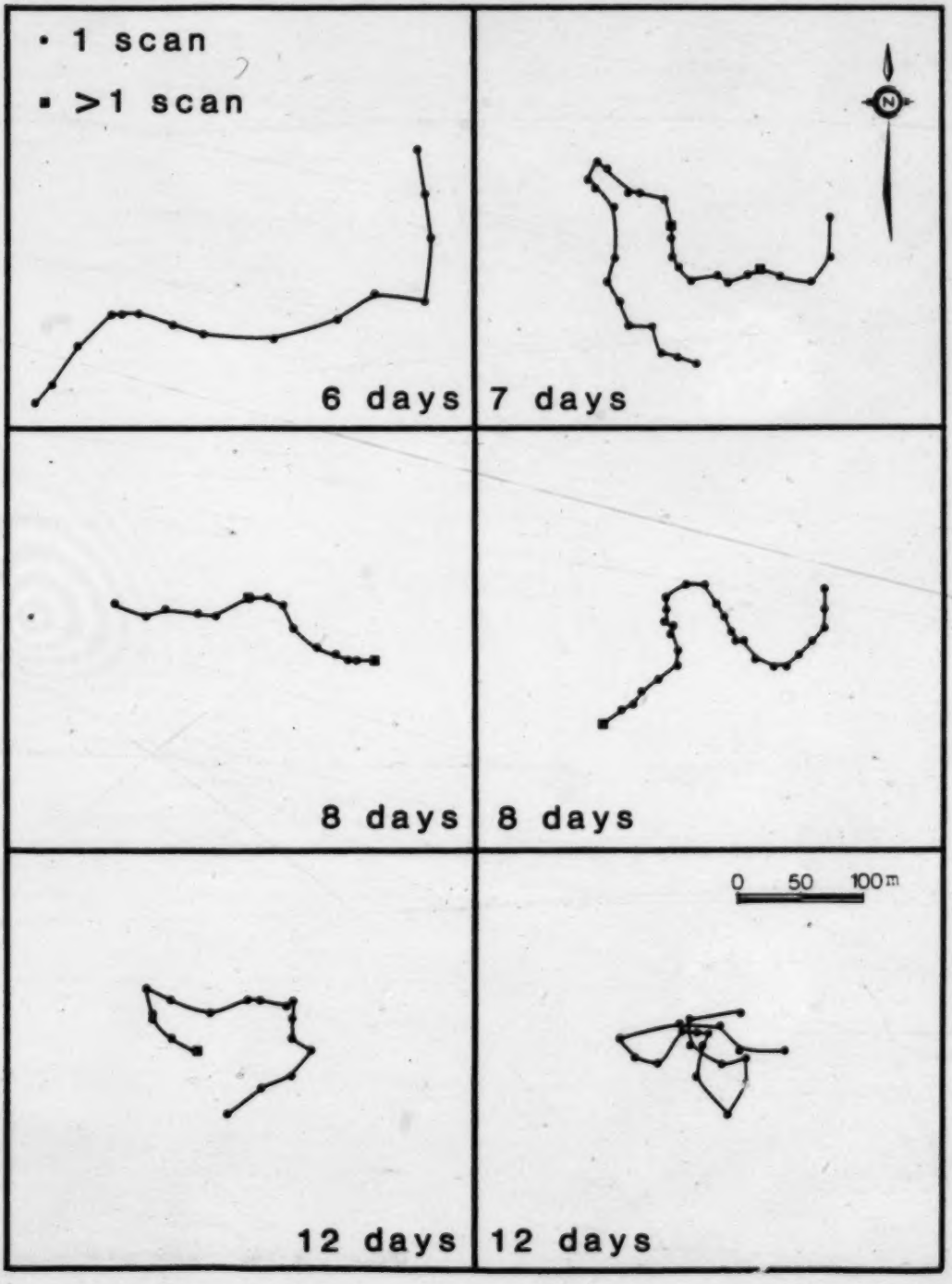


Figure 7B. Patterns of movement for spruce grouse broods observed for > 3 hours in southwestern Alberta (12 - 28 days of age).

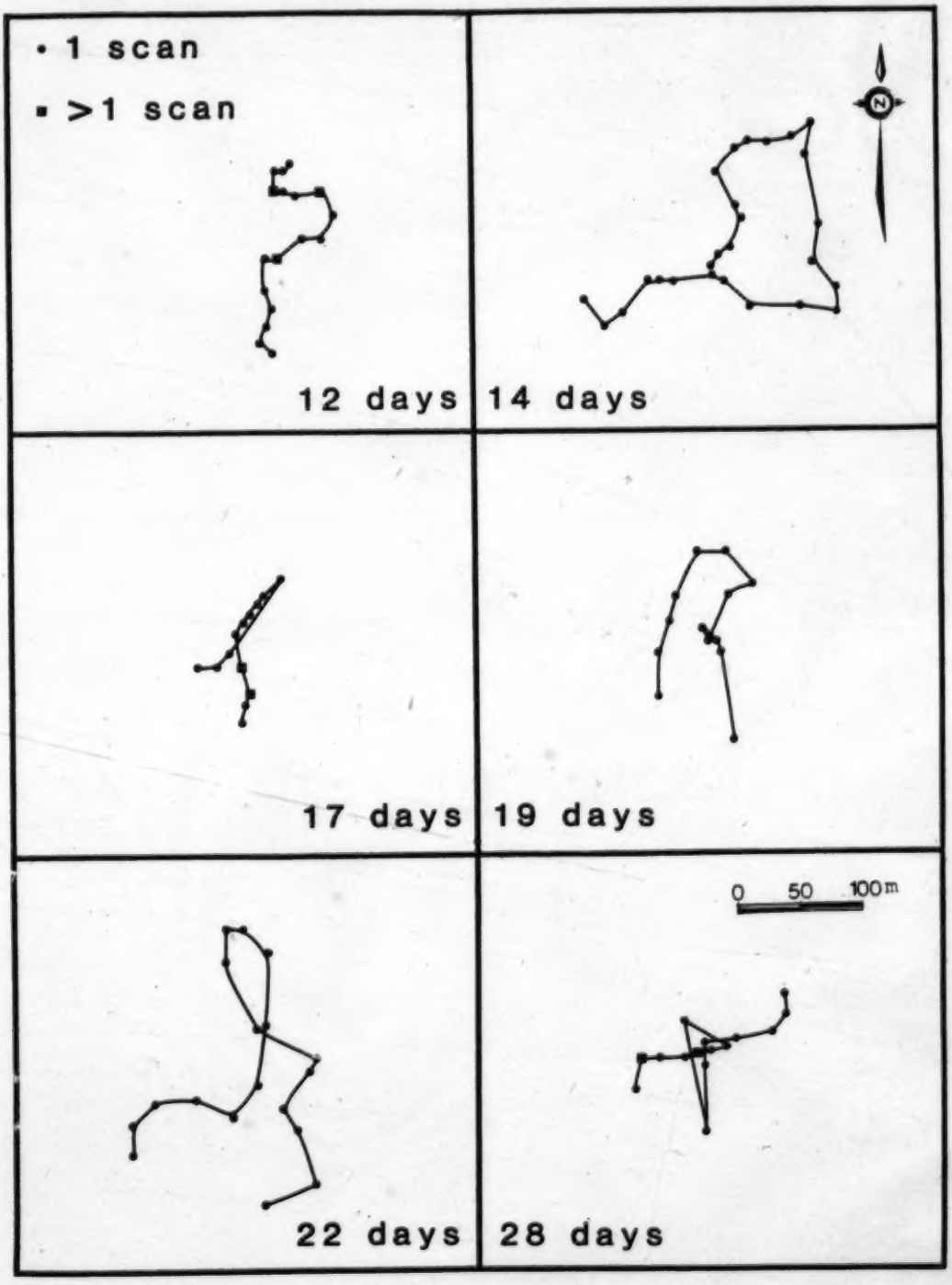


Figure 7C. Patterns of movement for spruce grouse broods observed for > 3 hours in southwestern Alberta (32 - 48 days of age).

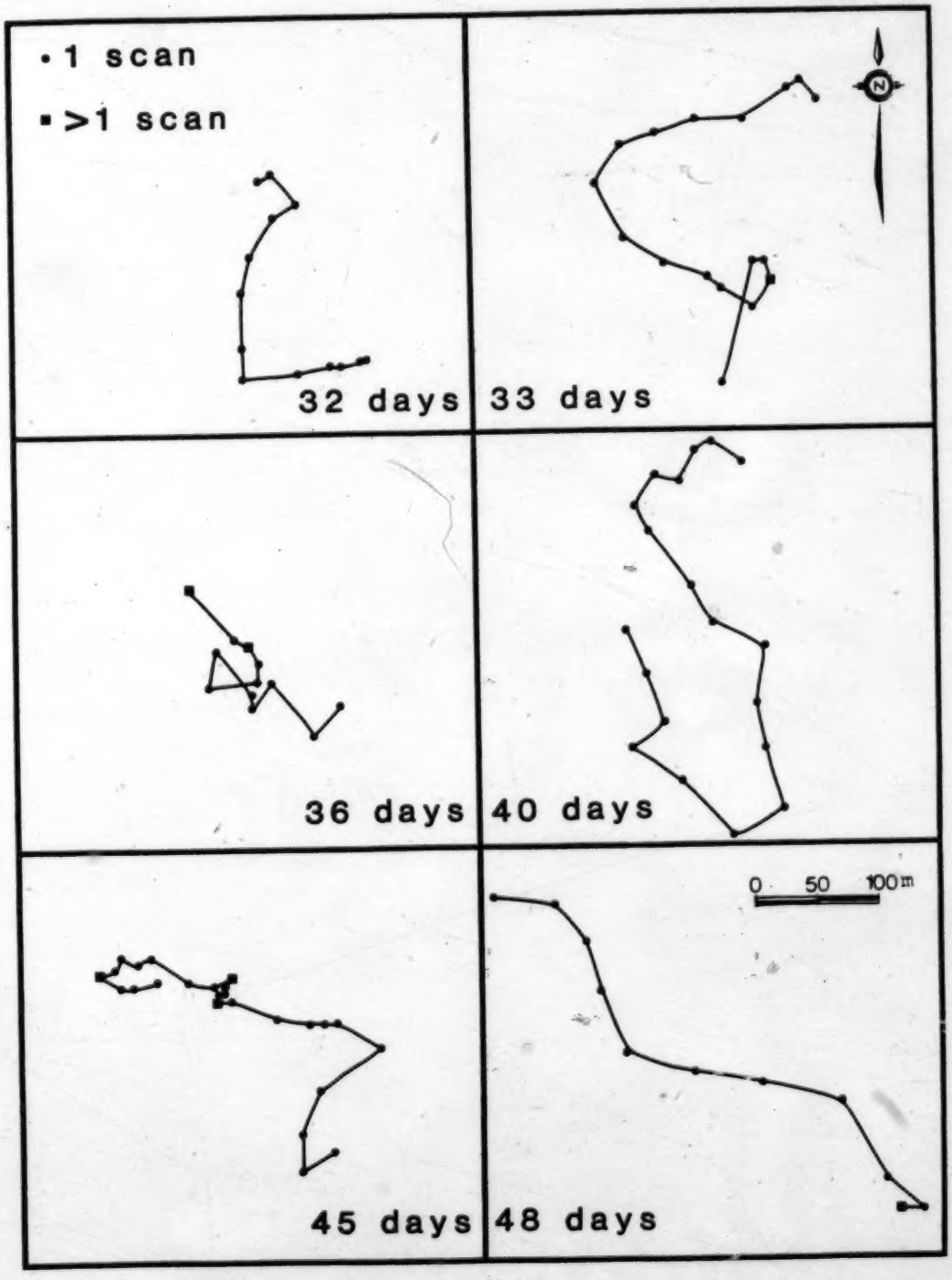
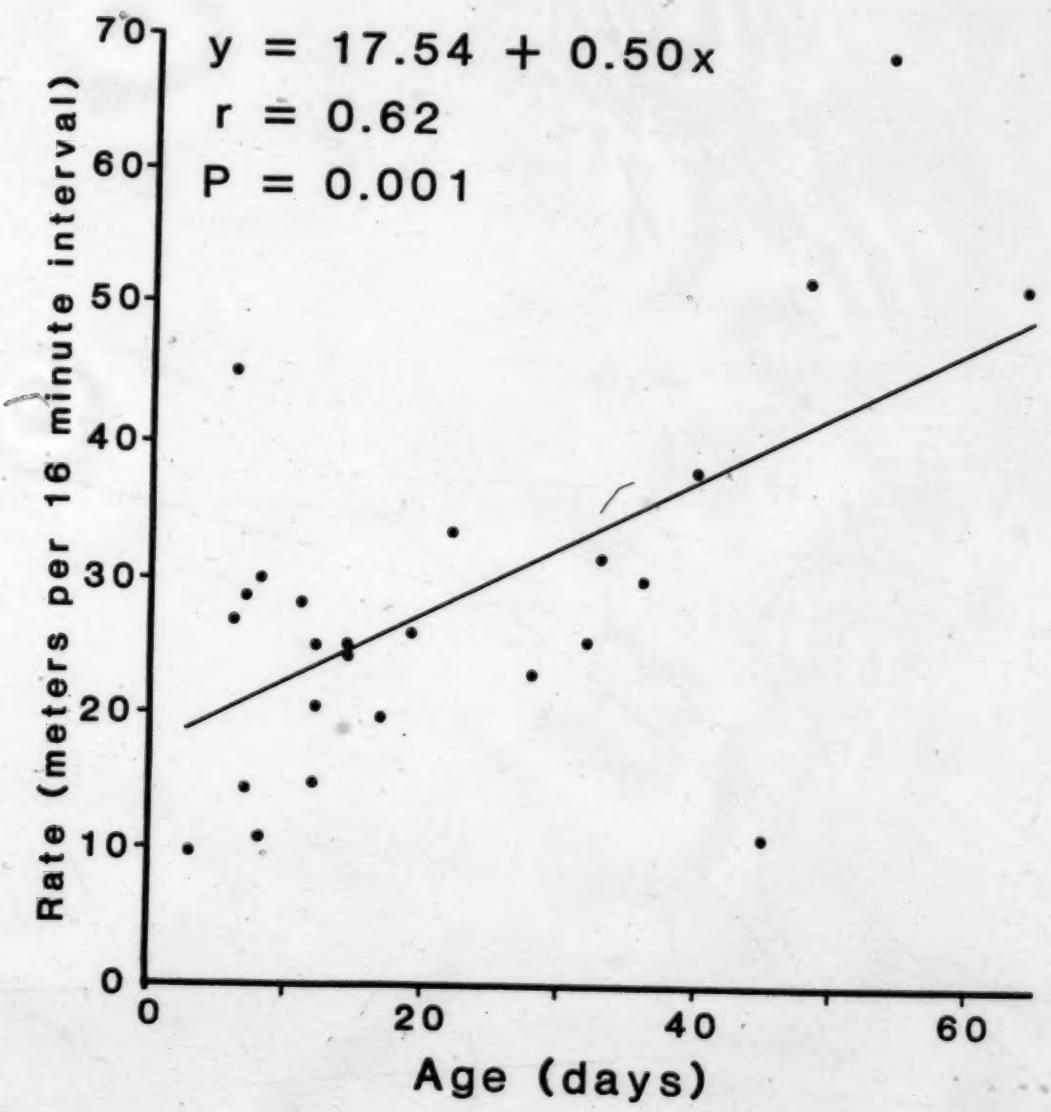


Figure 8. Rate of movement by spruce grouse broods of different ages in southwestern Alberta (periods when brooding occurred were excluded).

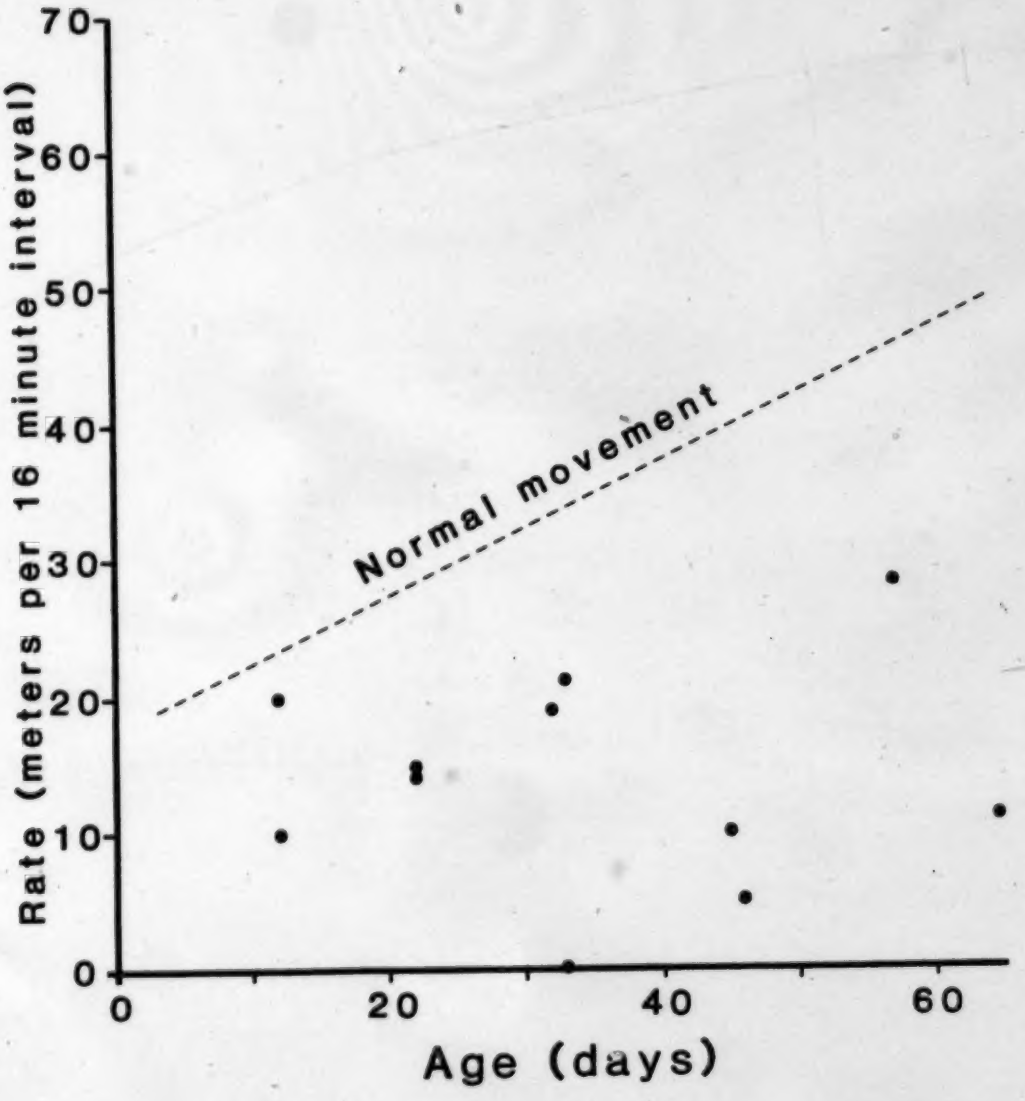


also have slowed the hen's movement. In all 11 cases in which the hen's movement was noted following the recording of purring calls, the distance moved by the brood hen was less than that expected ($P < 0.05$; Chi-square contingency table), based on normal rates of brood movement (Fig. 9). Although the brood hen's slower movement in open areas may be a response to the purring calls of chicks, other factors, such as her perception of good feeding habitat and/or greater vigilance because of increased predation vulnerability, could also cause slower movements.

As observed by McCourt (1969) and Alway (1977), brood hens typically viewed the feeding brood from elevated positions such as logs. The hens would often remain alert in such locations and respond to chicks with heep calls. If potential predators such as raptors (Accipitrinae), red squirrels (*Tamiasciurus hudsonicus*), or the researchers were observed, the hen would utter hum calls similar to those recorded by Alway (1977). Although Alway observed alarm calls given in response to more immediate dangers (raptors or closely approaching ground predators) than when the hum call was uttered, the same call was not distinct in this study. In the case of red squirrels, brood hens were observed on two occasions visually and vocally threatening the squirrel by erecting their feathers, fanning their tail, and charging within 0.5 m of it while uttering the cantus. In response to the approach of a researcher, the hen typically uttered the cantus and gave distraction displays if the chicks were less than 2 weeks of age and unable to fly well. The first weak flight by a juvenile spruce grouse was observed at 8 days of age, while flight at 7 days was observed by Stoneberg (1967) and 14 days by Alway (1977). The chicks generally responded to hum calls by becoming motionless (or alert) and silent. The response to immediate potential danger was similar but frequently included escape behaviour by the chicks (running, flying, and/or hiding).

Among juveniles, hum calls appeared to be given only by females, as suggested by Alway (1977). By contrast, no juveniles of either sex were recorded giving alarm calls. The sex-specific use of hum calls may be expected if the calls are an important part of the vocal reperoire of brood hens. Among juvenile females the hum call was first recorded at 45 days of

Figure 9. Rate of movement by spruce grouse broods of different ages in southwestern Alberta immediately following a chick purring call (normal movement line taken from Fig. 8 for comparison).



age. Females of all ages were heard giving hum calls during the fall, winter, and early spring while in flocks with other related and/or unrelated spruce grouse. The hum call seemed to have the same effect in flocking situations as it had in broods; it typically illicited silence and immobility from flocked birds.

Loafing behaviour

Loafing behaviour was a major component of the behavioural repertoire of juvenile spruce grouse (Fig. 2) and specifically included loafing, preening, dust-bathing, and flapping run behaviours. Chicks spent most of their loafing time sitting on the ground in the sunshine. Most preening was done in such situations. Occasionally juveniles, along with the brood hen, dust-bathed. The earliest a chick was observed dust-bathing was at 6 days of age, similar to that recorded for ruffed grouse (*Bonasa umbellus*)(Maxson 1978), and red grouse (*Lagapus lagapus scoticus*)(Watson and Jenkins 1964).

Flapping run behaviour was also characteristic of loafing situations. Although previously linked to male juveniles about the time of brood break-up (Alway 1977), the behaviour was observed here in chicks as early as 2 days of age. Likewise, intense forms of flapping run behaviour were observed for both sexes of juveniles and even in a 4-year-old female. In the latter case, the female vigorously displayed the flapping run behaviour for 30 seconds after alighting from a tree in which the night had been spent. This behaviour appeared to be contagious among juveniles (Alway 1977) and was most often observed immediately after loafing or brooding.

Additional behaviour

In addition to brooding, feeding, and loafing, juveniles displayed other behaviour patterns related to intraspecific interactions and/or potential breeding. Although interactions occurred in the broods observed, they were neither sufficiently overt nor frequent enough for me to determine dominance heirarchies. The most notable behaviour associated with

interactions was the jerky crouch (referred to as nervous crouch by Alway 1977). Although Alway observed it frequently in chicks at more than 61 days of age, I observed it four times in chicks 43-48 days old. On two occasions a juvenile female gave the jerky crouch when approached closely by her brood hen. The other two occurred among juvenile males, apparently in response to a closely approaching male sibling that was displaying. All four situations appeared to be similar to those observed by Alway (1977) and may have been a subordinate bird's response to a more dominant individual.

Like the jerky crouch, the display walk cum tail swaying and rush cum momentary tail fanning were both observed first with a 45 day old male, as opposed to being observed first by Alway (1977) with 90 day old juvenile males in captivity. Although the example from this study apparently occurred as part of an interaction (within a brood of four males), the same behaviours were observed by males with at least one female nearby.

Interactions among juveniles did not appear to be common at any time of the brood season, including the time around brood break-up (median of 4 September for males and 15 September for females; Paper 2). They were seldom observed, and were spread throughout the entire brood period. Although Alway and Boag (1979) observed an increase in aggressive interactions in October among captive juveniles, broods generally break up about a month earlier in the wild. Additionally, a high frequency of aggressive interactions, such as those observed by Watson and Jenkins (1964) in red grouse and Alway and Boag in spruce grouse, may be an artifact of captivity. Wild situations may permit the essentially unrestricted movement of chicks and consequently an easy avoidance of potential interactions (Zwickel 1967).

CONCLUSION

The results of this study describe the behavioural ontogeny of juvenile spruce grouse from their date of hatch to brood break-up. Early brood behaviour is characterized by a dependence of the juveniles on brooding by the brood hen. As brooding becomes less

important (chicks > 30 days of age), juveniles spend more time feeding (about 70% of their time). Various loafing behaviours tend to be displayed by chicks of any age. Additional behaviours related to sexual displays and aggressive interactions appeared to be added to the behavioural repertoire of chicks at 40-50 days of age.

Brood hens appear to respond automatically to the sreep, sury, seer, and purring calls of any chicks, both their own and those of other hens. Conversely, chicks appear to be able to recognize their own brood hen, but do adapt to a new hen when neccessary. Although apparently influencing much of the behaviour of brood hens, chicks probably do not affect other aspects of the brood hen's behaviour such as direction of movement.

The cohesion of the broods in this study appeared to gradually weaken until the time broods break up. Hen-chick and intersibling distances increased throughout the brood season. Likewise, the hen-chick distances required to elicit a seer call by the chicks also increased with age. A notable lack of aggressive interactions at the time of brood break-up suggests that they are probably not important in actually causing the break-up. Although the above observations do not eliminate the potential importance of aggressive interactions within broods, they do indicate that other factors may be more important in explaining the timing of brood break-up.

LITERATURE CITED

ALLEN, H. M., C. BOGGS, E. NORRIS, AND M. DOERING. 1977. Parental behaviour of captive willow grouse, *Lagopus l. lagopus*. Ornis Scand. 8:175-183.

ALTMANN, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:227-267.

ALWAY, J. H. 1977. A study of social behaviour relating to brood break-up and dispersal in Franklin's grouse under captive conditions. M.S. Thesis. Univ. of Alberta, Edmonton. 107p.

ALWAY, J. H., AND D. A. BOAG. 1979. Behaviour of captive spruce grouse at the time broods break up and juveniles disperse. Can. J. Zool. 57:1311-1317.

AULIE, A. 1976. The pectoral muscles and the development of thermoregulation in chicks of willow ptarmigan (*Lagapus lagapus*). Comp. Biochem. Physiol. 53A:343-346.

BOAG, D. A., K. H. MCCOURT, P. W. HERZOG, AND J. H. ALWAY. 1979. Population regulation in spruce grouse: a working hypothesis. Can. J. Zool. 57:2275-2284.

BOGGS, C., E. NORRIS, AND J. B. STEEN. 1977. Behavioural and physiological temperature regulation in young chicks of the willow grouse (*Lagopus lagopus*). Comp. Biochem. Physiol. 58A:371-372.

BOWMAN, T. J., AND R. J. ROBEL. 1977. Brood break-up, dispersal, mobility, and mortality of juvenile prairie chickens. J. Wildl. Manage. 41:27-34.

ELLISON, L. N. 1971. Territoriality in Alaskan spruce grouse. Auk 88:652-664.

ERIKSTAD, K. E., AND T. K. SPIDSO. 1982. The influence of weather on food intake, insect prey selection and feeding behaviour in willow grouse chicks in northern Norway. Ornis Scand. 13:176-182.

HARJU, H. J. 1969. Accoustical communication of the spruce grouse. M. S. Thesis. N. Michigan Univ., Marquette. 108p.

HERZOG, P. W., AND D. A. BOAG. 1978. Dispersion and mobility in a local population

of spruce grouse. J. Wildl. Manage. 42:853-865.

HERZOG, P. W., AND D. M. KEPPIE. 1980. Migration in a local population of spruce grouse. Condor 82:366-372.

HJORTH, I. 1970. Reproductive behaviour in Tetraonidae with special reference to males. Viltrevy 7:181-596.

JOHNSGARD, P. A. 1983. The grouse of the world. Univ. of Nebraska Press, Lincoln. 413p.

KEPPIE, D. M. 1977. Inter-brood movements of juvenile spruce grouse. Wilson Bull. 89:67-72.

KEPPIE, D. M. 1979. Dispersal, overwinter mortality, and recruitment of spruce grouse. J. Wildl. Manage. 43:717-727.

LUMSDEN, H. G. 1961. Displays of the spruce grouse (Aves:Tetraonidae). Can. Field Nat. 75:152-160.

MACDONALD, S. D. 1968. The courtship and territorial behavior of Franklin's race of the spruce grouse. Living Bird 7:5-25.

MAXSON, S. J. 1978. Growth and behavior of ruffed grouse chicks. Loon 106-112.

MCCOURT, K. H. 1969. Dispersion and dispersal of female and juvenile Franklin's grouse in southwestern Alberta. M. S. Thesis. Univ. Alberta, Edmonton. 137p.

MCCOURT, K. H., AND D. M. KEPPIE. 1975. Age determination of juvenile spruce grouse. J. Wildl. Manage. 39:790-794.

NUGENT, D. P., AND D. A. BOAG. 1982. Communication among territorial female spruce grouse. Can. J. Zool. 60:2624-2632.

PEDERSEN, H. C., AND J. B. STEEN. 1979. Behavioural thermoregulation in willow ptarmigan chicks, *Lagopus lagopus*. Ornis Scand. 10:17-21.

PYNNONEN, A. 1954. Beitrage zur Kenntnis des Lebensweise des Haselhuhns, *Tetrastes bonasia* (L.). Pap. Game Res., 12:1-90.

STONEBERG, R. P. 1967. A preliminary study of the breeding biology of the spruce grouse

in northwestern Montana. M. S. Thesis. Univ. Montana, Missoula. 82p.

THEBERGE, J. B., AND G. C. WEST. 1973. Significance of brooding to the energy demands of Alaskan rock ptarmigan chicks. Arctic 26:138-148.

WATSON, A., AND D. JENKINS. 1964. Notes on the behaviour of the red grouse. Br. Birds 57:137-170.

WOOD-GUSH, D. G. M. 1955. The behaviour of the domestic chicken: a review of the literature. Brit. J. Anim. Behav. 3:81-110.

ZWICKEL, F. C. 1967. Early behavior in young blue grouse. Murrelet 48:2-7.

ZWICKEL, F. C., AND J. F. BENDELL. 1967. A snare for capturing blue grouse. J. Wildl. Manage. 31:202-204.

PAPER 2: THE FALL PHASE OF DISPERSAL IN JUVENILE SPRUCE GROUSE

INTRODUCTION

The dispersal of spruce grouse from their place of hatch to their place of breeding or attempted breeding is divided into two descrete phases: fall and spring (Keppie 1975). The two phases are separated by a winter period during which relatively little movement occurs. Keppie (1979) studied two general characteristics of the fall phase of dispersal, distance moved and emigration rate (rate of disappearance from the study area). He considered birds that moved beyond the boundaries of his study area as emigrants and those that remained on the study area as non-emigrants. Although the emigration rate of males (41%) recorded by Keppie was significantly lower than that of females (75%), the sexes did not differ in the distances moved within the study area (Keppie 1975). Nevertheless Keppie suggested that the larger emigration rate of females was probably related to their greater overall dispersal distances. Thus, dispersal distances of the two sexes measured within the boundaries of the study area, are probably unrepresentative of the true distances moved by the birds (the area encompassed was too small relative to potential distances moved).

Apart from documentation of fall movements in juvenile spruce grouse, the causes of the observed variability in patterns of movement, such as with distances moved, has been suggested to be the result of intraspecific interactions and/or innate behavioural differences (Herzog and Boag 1977, 1978, Alway and Boag 1979, Keppie 1979, 1980). Another factor that may influence the fall phase of dispersal and hence 'disappearance' rates (Keppie 1979) of juvenile spruce grouse, is the probability of encountering patches of winter habitat that would bring dispersing birds to a stop. The distribution and size of such blocks of habitat has not previously been considered despite frequent observations of winter flocking in this grouse (Ellison 1973, Keppie 1975). The extent to which juveniles move with their migrating mother is possibly an important aspect in whether juveniles stop in the first wintering areas encountered. Thus, the timing of events relative to brood break-up and dispersal is also

important for the analysis of fall dispersal. Although Keppie (1975) observed juveniles moving with their migrating brood hens, the date of brood break-up in relation to the timing of adult female migration was not examined in describing patterns of movement associated with the fall phase of dispersal. Because a large proportion of brood hens is migratory (55% according to Herzog and Keppie 1980), and dates of migration and brood break-up may overlap, timing of dispersal may influence distances moved and deserves consideration.

This paper re-examines dispersal distances and disappearance rates of juvenile spruce grouse during the fall. Previously ignored aspects of juvenile and brood hen behaviour at the time of brood break-up, as well as possible concentrations of wintering grouse, are considered because of their potential influence on fall movements.

METHODS

Spruce grouse have been censused and/or radio-tracked from 1965 to 1984 near the R. B. Miller Biological Station (50° 39' N, 114° 39' W) 27 km west of Turner Valley, Alberta. The main study area consisted of 555 ha of forest dominated by lodgepole pine (*Pinus contorta*), with scattered clumps of white spruce (*Picea glauca*) and poplar (*Populus* spp.)

Birds were noosed (Zwickel and Bendell 1967) and individually marked with color-coded leg bands. Radio transmitters were attached to females in 1974-5, 1977, and 1980-4 and to juveniles in 1975 and 1982-3. Locations of birds were plotted using a large grid system superimposed over air photos.

Grouse are categorized as juveniles (< 6 months), yearlings (6-15 months), or adults (> 15 months). Designation of seasons was based on aspects of behaviour, such as movement and dispersion within a season (Herzog and Boag 1978), and timing of migration and dispersal movements (Herzog and Keppie 1980), and were as follows: Winter (15 Oct. - 31 Mar.); and Summer (15 May - 15 Aug.). These designations with up to 2 months between them enabled me to avoid confusion between early and late movements, either dispersal or migration, and normal daily movements within summer or winter ranges.

Median dates for the initiation of adult migration in the fall were determined by examining daily locations of radio-tagged adult females only. The intensity of search effort on the study area exceeded that beyond its artificial boundaries, and consequently it was necessary to distinguish birds that remained on the area from those that moved off the area for part of the year. Any adult female having spatially separate winter and summer ranges on the study area was classed as an on-area migrant, whereas those crossing the boundaries of the study area were classed as off-area migrants. Brood break-up dates for juveniles were designated as the midpoint between a bird's last sighting in the brood and its first sighting away from the brood hen (only those cases for which the interval was 14 days or less were considered).

Dispersal distances of juveniles in the fall were determined by calculating the straight-line distance between the median locations (median of x and y coordinates) of all sightings on their brood and winter ranges. Disappearance rates were calculated by dividing the number of juveniles missing from the study area in winter, by the number of juveniles known to be alive on the study area in late summer. A mortality rate of 15% for the 2-month period during and after brood break-up, based on the death of 4 of 27 radio-marked birds, was incorporated into the estimate. The data used for calculating fall disappearance rates were only compiled for those years in which the main area was censused during both the summer and winter (1970-3, 1982-3). Other data on dispersal distances were analyzed for all years. Most birds residing on the study area were probably found while censusing (Boag and McKinnon 1982), because almost all radio-tagged birds on the study area were found by using normal censusing techniques in addition to radio telemetry.

Locations of areas used by grouse in winter were determined by plotting on a map the median wintering locations (based on a minimum of three sightings) of each adult bird. Wintering areas were delineated when the median locations of three or more adult grouse occurred in a cluster in which the distance between neighbours did not exceed 80 m (mean radius of the winter range of radio-tracked adults; Herzog and Boag 1978). A perimeter was drawn around each cluster enclosing all its median locations as well as a boundary area

extending 80 m from the outer medians of the cluster, thus encompassing the area used by peripherally located birds.

RESULTS

Characteristics of the fall phase of dispersal

Dispersal distances for juvenile spruce grouse during the fall ranged up to at least 6 km (Fig. 1). Based on data from juveniles without radios, there was no difference in distances moved by males and females, but females moved further than males when only radio-tracked juveniles were considered (Table 1). Having moved off the study area, radio-tracked juveniles were easier to find than leg-banded birds; using the former reduced the sampling bias caused by censusing a fixed area (the diameter of which was smaller than the dispersal distance of much of the population). The disappearance rate of females (75.8%; n=103) was significantly higher ($P < 0.001$; Chi-square contingency table) than that of males (52.1%; n=114). Both rates were similar to those recorded by Keppie (1979).

Association with wintering areas

Wintering areas cover less than 15% of the study area (Figure 2) yet enclose 81% of all median locations of wintering adults. The remaining 19% of the median locations were of single birds (and hence did not qualify for the definition of a wintering area) scattered widely throughout the rest of the study area. Similarly, 81% of juvenile males (n=91) and 86% of juvenile females (n=87) had median winter locations within the boundaries of wintering areas. Juvenile males did not differ from females in their proximity to wintering areas ($P > 0.10$; Chi-square contingency table). However, both had their median locations on wintering areas more frequenty than would be expected if they were distributed randomly throughout the study area ($P < 0.001$ for both males and females; Chi-square contingency table).

Figure 1. Distribution of fall dispersal distances for female (n = 42) and male (n = 88) juvenile spruce grouse in southwestern Alberta, 1965 - 1984.

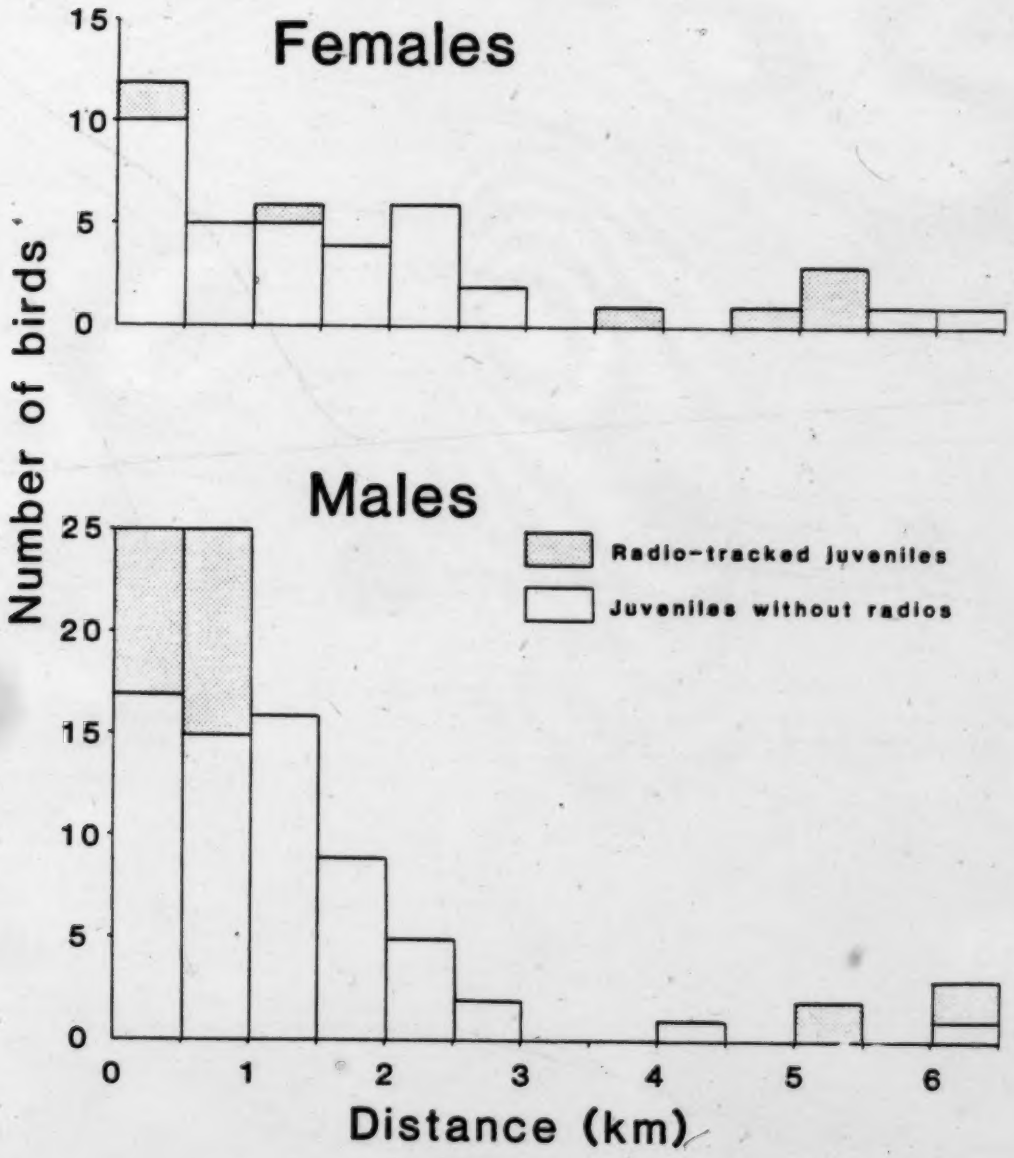
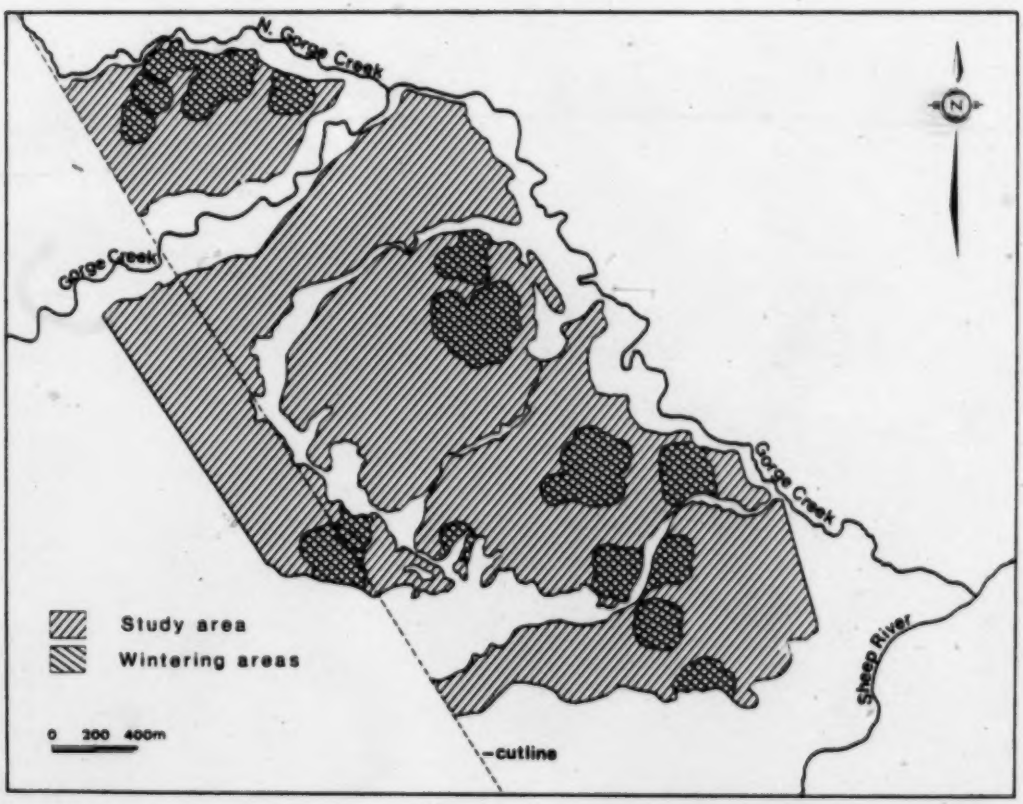


Table 1. Median distances (m) for the fall phase of dispersal for juvenile spruce grouse in southwestern Alberta.

Category	Male (N)	Female (N)	P^1
Radio-tracked juveniles	650 (22)	4974 (9)	0.048
Juveniles without radios	1059 (66)	1085 (33)	0.447

[1]Mann-Whitney U-test (2-tailed).

Figure 2. Location of spruce grouse wintering areas on the southwestern Alberta study area.

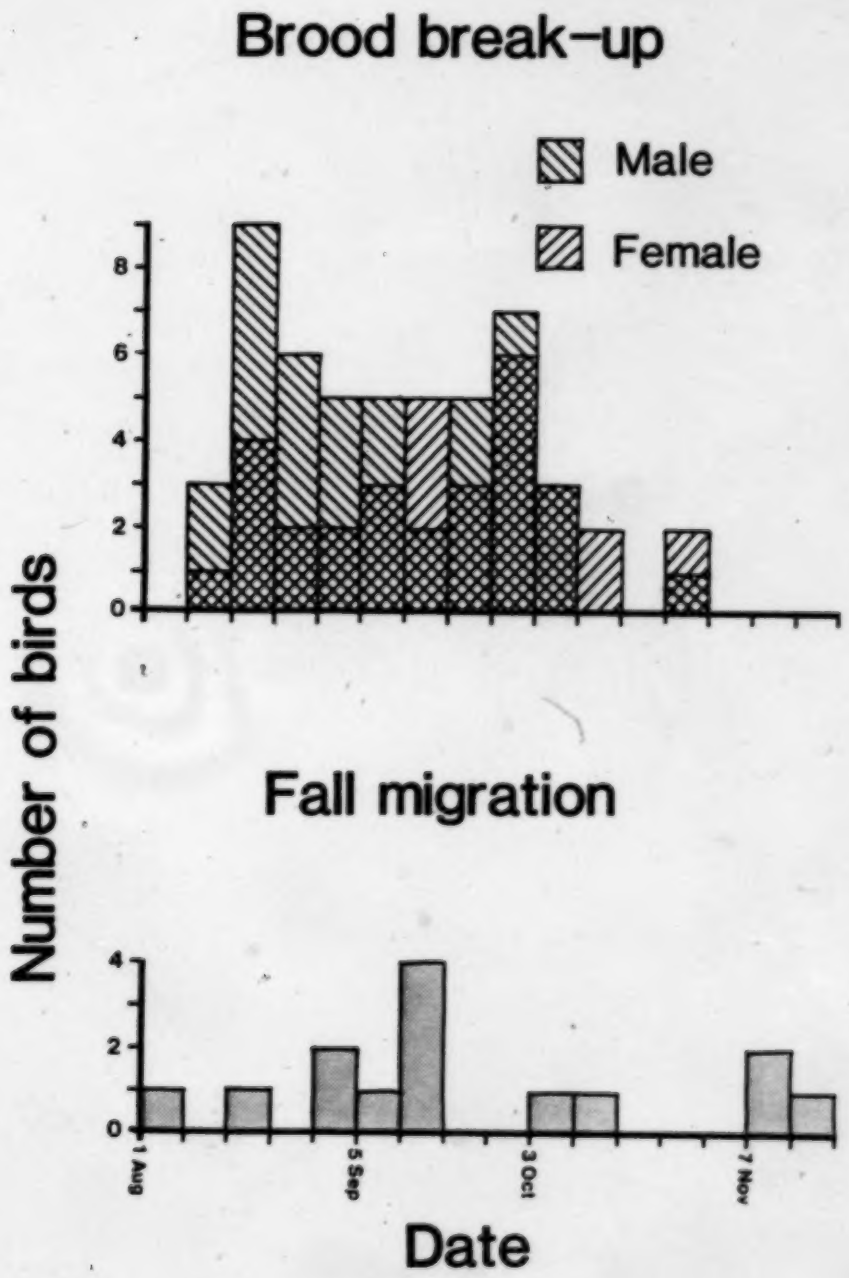


Timing of the fall phase of dispersal

The median date of migration for brood hens was 13 September (range of 3 Aug. - 18 Nov.; n=14). The median brood break-up date for juvenile females (15 September; range = 8 Aug. - 26 Oct.; n=33) was significantly later (P = 0.026; Mann-Whitney U-test) than that for juvenile males (4 September; range = 13 Aug - 23 Oct.; n=46). The difference between the sexes in date of brood break-up, and the fact that date of brood hen migration overlapped that of brood break-up, suggest the potential importance of the relative timing of the two events in the observed patterns of the fall phase of dispersal (Fig. 3). For example, the fall migration dates of 14 radio-tracked adult females were compared with the median dates of brood break-up for juvenile males and females. This comparison revealed that 9 of 14 females would have migrated before the median date of brood break-up of female chicks (15 September), and 4 of 14 before the median date of brood break-up of male chicks (4 September). If the 14 radio-tracked females used in this study are representative of brood hens, this would suggest that approximately 64% of female and 29% of male juveniles would still be in broods at the onset of the brood hen's migration and hence could potentially move with their migrating mother.

In this study 47% of the adult females on the study area in the summer migrated off the area in the fall (15 of 32 radio-tracked females). The mean off-area migration distance of 2576 m was longer than the mean on-area distance of 496 m (P = 0.007; Mann-Whitney U-test). The latter distance was 57% of the mean dispersal distance of juveniles between brood and winter ranges on the study area (880 m; n = 72), suggesting that even movement of juveniles with their on-area migrant brood hens potentially could affect dispersal distances. The large overlap in dates of brood break-up and brood hen migration suggests that the potential for juveniles to move with their migrating brood hen is considerable. Despite the previous observations of juveniles with migrating brood hens (Keppie 1975), the importance of these movements on the disappearance rates and fall dispersal distances of juveniles has not been considered.

Figure 3. Distribution of dates of brood break-up for juveniles and dates of fall migration for radio-tagged brood hens in southwestern Alberta.



A more detailed analysis of emigrants or off-area dispersers supports the above suggestions. Of 28 juveniles that dispersed more than 2 km, 20 had known off-area migrant brood hens; the status of the brood hens of the remaining 8 was unknown. For the 13 juveniles moving more than 3 km, all had off-area migrant brood hens (13 chicks among 7 different broods). Of these 13, 10 (6 females and 4 males) had radio-tracked brood hens (4 different hens) and all 10 were known to have moved with their migrating mother.

DISCUSSION

The existence of areas where adults concentrate in winter, although previously unrecorded and generally relatively small in size, may be very important in influencing the settlement of juveniles in winter. Restricted areas of preferred winter habitat, as suggested by Ellison (1976), Herzog (1977), Paterni (1979), Herman (1980), and Robinson (1980), and the formation of winter flocks, as described by Ellison (1973) and Keppie (1975), may be primary factors influencing the use of space in winter. The evidence presented here shows that the distribution of juveniles in winter was not random but that they were associated with the same areas used by wintering adults. This association may reflect a tendency of juveniles to flock with other spruce grouse and/or to select the same habitat.

The association of juveniles with specific wintering areas suggests that dispersal distances and disappearance rates in the fall could reflect the availability of these areas along the paths of dispersing birds. However, even if wintering areas are used as destinations for moving juveniles, they do not fully explain the large disappearance rates. Moreover, they do not provide a possible explanation for sexual differences in disappearance rate and dispersal distance.

Examination of the timing of events during the brood break-up and fall dispersal period provides a possible explanation for characteristics of the fall phase of dispersal in spruce grouse. The overlap in the timing of brood break-up and brood hen migration suggests that it may be relatively common for juveniles to move with their migrating brood hens (a large

percentage of females probably migrate before their broods break up). Field observations of juveniles accompanying their migrating mothers (Keppie 1975, this study) agree with this suggestion, and explain why variation in dispersal distances within broods may be less than between them (Keppie 1980). Analysis of distances of dispersal during the fall for radio-tracked juveniles shows that females move significantly farther than males. Similarly, females have significantly greater disappearance rates than males. The proportionally longer movements made by females than males support Keppie's (1975) speculation based on emigration rates alone. The fact that females leave the brood later than males, and that juveniles may accompany their migrating brood hen if migration precedes brood break-up, suggests a reason for the difference in distance moved and disappearance rate for the two sexes. The significance of this phenomenon is that migrating brood hens would be more likely to migrate in the company of their female than their male chicks.

The most apparent and potentially important factors affecting the fall phase of dispersal in juvenile spruce grouse were examined in this study. Additional factors that were not considered in this study may also be operating. For example, dominance-subordinance interactions within a sex and/or sex and age class may influence the spatial organization of spruce grouse in the winter. Intraspecific interactions have been observed in the field (Schroeder, in prep.), but their implications for spacing behaviour are so far based on indirect evidence (Ellison 1973, Herzog and Boag 1978, Alway and Boag 1979).

Alway (1977) suggested that dominance hierarchies, possibly formed in the brood, may have an effect on patterns of dispersal, such as distances moved. However, he observed few aggressive interactions until after the fall dispersal period, and suggested that innate behavioural differences among juveniles were probably more important in causing differences in fall movements. Similarly, Keppie (1979) found that the fall phase of dispersal was not related to grouse densities, apparently because of equal emigration and immigration. If movement were influenced by aggresssive interactions, a positive relationship between density and distance and/or emigration rate would be expected because of the increased probability

and/or necessity of encountering conspecifics. Keppie (1980) also found that the variability for distances moved during the fall phase of dispersal for juveniles within broods was less than among broods, potentially supporting the idea that a genetic component of behaviour might explain the variability between broods. However, the variability observed by Keppie may also be explained by the sharing of similar environments by members of each brood, such as the quantity and/or quality of wintering areas near the brood's summer range. Likewise, variation in attributes of the brood hen such as hatchdate (age of the juveniles) and behaviour associated with brood cohesion and/or migration, would produce the same effect.

The fall phase of dispersal is characterized by a movement in which females move both farther and more frequently than males. Whether the increased movement of females plays an important part in increasing gene flow (Howard 1960, Johnston 1961, Murray 1967), colonizing suitable habitats (Dice 1952), and/or regulating the population size (Errington 1956, Lidicker 1962, French *et al.* 1968, Christian 1970, Myers and Krebs 1971), remains an unanswered question. Despite the lack of information on the ultimate consequences of the fall phase of dispersal, the observations from this study suggest that the location and/or timing of brood break-up and location of wintering areas are proximal factors that could influence the nature of the dispersal movement. If juvenile spruce grouse can be shown to stop at the first-encountered wintering area after brood break-up, it would suggest that other factors such as dominance-subordinance interactions and/or innate differences in dispersal tendencies are of lesser importance than destination areas in affecting the patterns of fall dispersal.

LITERATURE CITED

ALWAY, J. H. 1977. A study of social behaviour relating to brood break-up and dispersal in Franklin's grouse under captive conditions. M.S. Thesis. Univ. of Alberta, Edmonton. 107p.

ALWAY, J. H., AND D. A. BOAG. 1979. Behaviour of captive spruce grouse at the time broods break up and juveniles disperse. Can. J. Zool. 57:1311-1317.

BOAG, D. A., AND D. T. MCKINNON. 1982. Spruce grouse. Pages 61-62 in D. E. Davies, ed., Handbook of census methods for terrestrial vertebrates. CRC Press, Inc., Boca Raton, Florida.

CHRISTIAN, J. J. 1970. Social subordination, population density, and mammalian evolution. Sci. 168:84-90.

DICE, L. R. 1952. Natural communities. Univ. Michigan Press. Ann Arbor. 547p.

ELLISON, L. N. 1973. Seasonal social organization and movements of spruce grouse. Condor 74:375-385.

ELLISON, L. N. 1976. Winter food selection by Alaskan spruce grouse. J. Wildl. Manage. 40:205-213.

ERRINGTON, P. L. 1956. Factors limiting vertebrate populations. Sci. 124:304-307.

FRENCH, N. R., R. Y. TAGAMI, AND P. HAYDEN. 1968. Dispersal in a population of desert rodents. J. Mammal. 49:272-280.

HERMAN, M. F. 1980. Spruce grouse habitat requirements in western Montana. Ph.D. Thesis. Univ. of Montana, Missoula. 181p.

HERZOG, P. W. 1977. Dispersion and mobility in a local population of spruce grouse. M.S. Thesis. Univ. Alberta, Edmonton. 98p.

HERZOG, P. W., AND D. A. BOAG. 1977. Seasonal changes in aggressive behavior of female spruce grouse. Can. J. Zool. 55:1734-1739.

HERZOG, P. W., AND D. A. BOAG. 1978. Dispersion and mobility in a local population of spruce grouse. J. Wildl. Manage. 42:853-865.

HERZOG, P. W., AND D. M. KEPPIE. 1980. Migration in a local population of spruce grouse. Condor 82:366-372.

HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Amer. Midl. Nat. 63:152-161.

JOHNSTON, R. F. 1961. Population movements of birds. Condor 63:386-389.

KEPPIE, D. M. 1975. Dispersal, overwinter mortality, and population size of spruce grouse. Ph.D. Thesis. Univ. of Alberta, Edmonton. 113p.

KEPPIE, D. M. 1979. Dispersal, overwinter mortality, and recruitment of spruce grouse. J. Wildl. Manage. 43:717-727.

KEPPIE, D. M. 1980. Similarity of dispersal among sibling male spruce grouse. Can. J. Zool. 58:2102-2104.

LIDICKER, W. Z. 1962. Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. Amer. Nat. 96:29-33.

MURRAY, B. J., JR. 1967. Dispersal in vertebrates. Ecology 48:975-978.

MYERS, J. H., AND C. J. KREBS. 1971. Genetic, behavioral and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecol. Monogr. 41:53-78.

PATERNI, M. 1979. Winter habitat selection by female spruce grouse in a mixed coniferous forest. M.S. Thesis. Univ. of Montana, Missoula. 96p.

ROBINSON, W. L. 1980. Fool hen: the spruce grouse on the Yellow Dog Plains. Univ. of Wisconsin Press, Madison. 221p.

ZWICKEL, F. C., AND J. F. BENDELL. 1967. A snare for capturing blue grouse. J. Wildl. Manage. 31:202-204.

PAPER 3: BEHAVIOURAL DIFFERENCES OF FEMALE SPRUCE GROUSE UNDERTAKING SHORT AND LONG MIGRATIONS

INTRODUCTION

Like many other Tetraoninae, spruce grouse migrate between winter and summer ranges (Herzog and Keppie 1980). The distance and direction of migration vary among individuals, as does the timing of movement, and the behaviour of migrating birds. The migration of adults has been suggested to be a retracing of movements made during their spring phase of dispersal as yearlings, when about 9 months old (Herzog and Keppie 1980). Dispersal, as described by Keppie (1975), is divided into fall and spring phases separated by a winter period during which relatively little movement occurs. Movement during these phases encompasses overall dispersal movement from the place of hatch to the first potential breeding area. Some ultimate consequences of such dispersal (increased gene flow, colonization of suitable habitats, population regulation) have been reviewed by Gaines and McClenaghan (1980), Greenwood and Harvey (1982), and Swingland and Greenwood (1983).

If migratory behaviour in adult spruce grouse is dependent upon their dispersal as yearlings in the spring, proximate causes of dispersal, such as inheritance (Myers and Krebs 1971) and intraspecific aggression (Herzog and Boag 1977, 1978, Alway and Boag 1979, Keppie 1979), may also influence subsequent patterns of migration. This study examines behavioural data from radio-tracked females exhibiting short and long-distance migratory movements. Although males also migrate, long-distance migrations are less frequent (Herzog and Keppie 1980), which makes studying them difficult.

Past research shows that long-distance migrations by female spruce grouse are predictable in consistency of direction and in rate of movement (Herzog and Keppie 1980). This suggests a relatively fixed behavioural pattern in these birds which may be different from those shown by females moving over short-distances. Likewise, the possibility that some juveniles select wintering areas where the potential for successful breeding the following spring

is high (Alway and Boag 1979), suggests that differences in dispersal, and hence migration, may be related to behavioural differences shown during the preceding winter. Since timing of migrations may be an important aspect of female behaviour associated with dispersal and subsequently migration, and since spruce grouse commonly flock in winter (Ellison 1973, Keppie 1975), both were examined and compared for females migrating short and long distances.

METHODS

Spruce grouse were radio-tracked in 1974-5, 1977, and 1982-4 near the R. B. Miller Biological Station 27 km west of Turner Valley, Alberta (50° 39' N, 114° 39' W). The main Gorge Creek study area consisted of 555 ha of forest dominated by lodgepole pine (*Pinus contorta*), with scattered clumps of white spruce (*Picea glauca*) and poplar (*Populus* spp.).

Birds of both sexes were noosed (Zwickel and Bendell 1967), individually marked with colored leg bands, and harnessed with radio transmitters. Radio-tagged birds were tracked with a hand-held yagi antenna and receiver. Locations were plotted using a large grid system superimposed on air photos. To help eliminate the potential biases inherent in typical censusing techniques, I used only behavioural data obtained from radio-tagged birds.

Grouse were classed as juveniles (< 6 months), yearlings (6-15 months), or adults (> 15 months). Designation of seasons was based on aspects of behaviour, such as movement and dispersion within a season (Herzog and Boag 1978), and timing of migration and dispersal movements (Herzog and Keppie 1980), and were as follows: Winter (15 Oct. - 31 Mar.); and Summer (15 May - 15 Aug.). These designations with up to 2 months between them enabled me to avoid confusion between early and late movements, either dispersal or migration, and normal daily movements within summer or winter ranges.

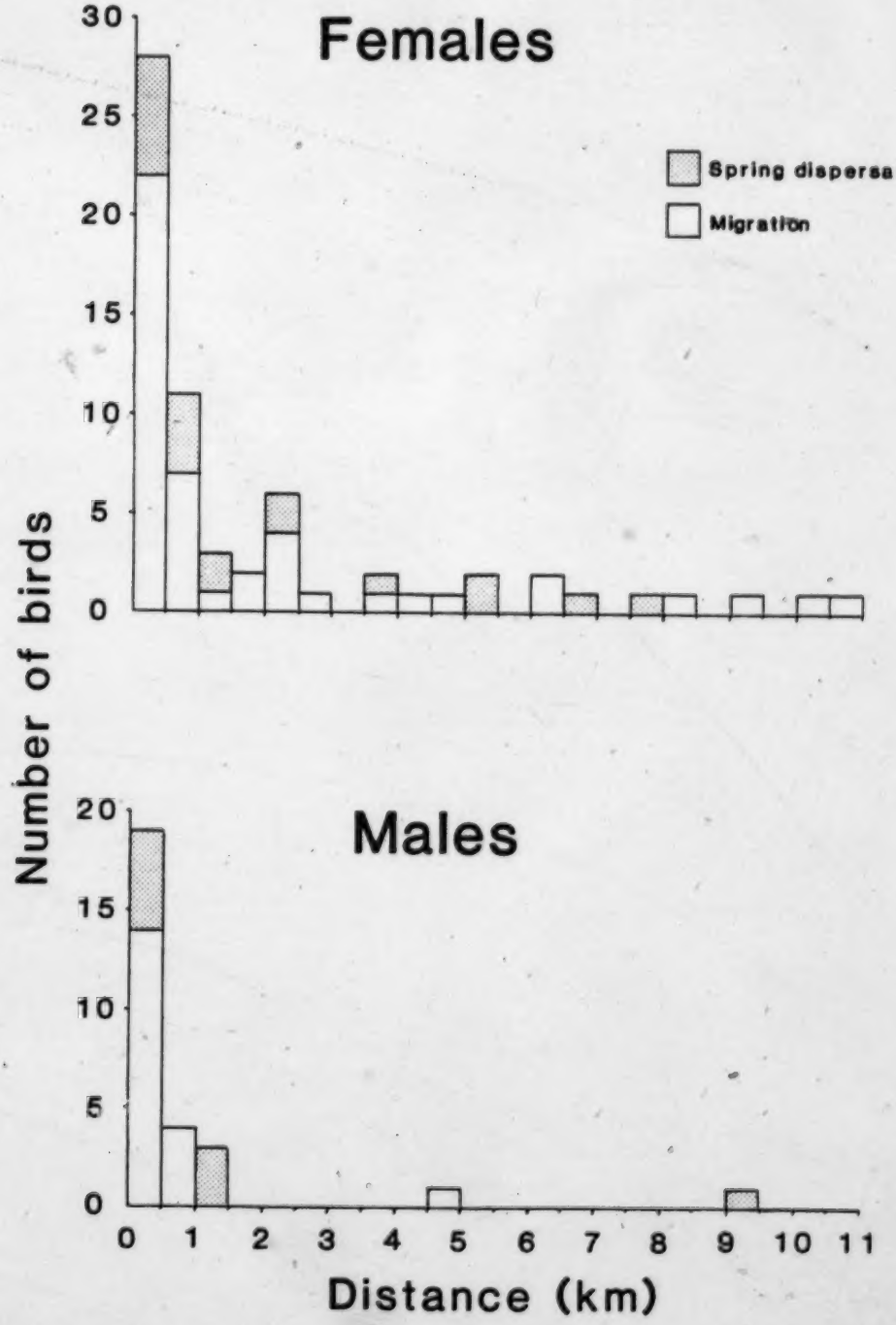
Distances moved during the spring phase of dispersal were estimated by measuring the distance between the median locations (calculated from all sightings) of a bird on its first winter range and subsequent breeding range. Distances migrated were estimated by measuring

the distance between the median location of summer and winter ranges as adults. A distance of 2 km, which is about one-sixth of the maximum migratory distance recorded, was used to separate long (> 2 km) and short (< 2 km) migrations. This was a natural dividing point in the skewed distribution of distances described (Fig. 1). Distances falling in the tail of the skewed distribution were classed as long-distance migrations. The 2 km separation point approaches the distance used by Herzog and Keppie (1980) to separate 'residents' from 'migrants', the equivalent of short-distance and long-distance migrants, respectively. Herzog and Keppie's classification is inappropriate because many of their 'resident' birds actually undertook seasonal migrations inside the boundaries of the study area.

The timing of migration was estimated for radio-tagged birds that were tracked frequently. Dates of migration were based on their (1) last day on wintering range, (2) first day on breeding range, (3) last day on breeding range, and (4) first day on wintering range. This method uses two dates for each movement (numbers 1 and 2 for spring migration and numbers 3 and 4 for fall migration). I compared the timing of these movements in long-distance and short-distance migrants. Because of the difficulty in differentiating between normal daily movement and short-distance migration, I excluded birds migrating < 400 m when analyzing the timing of migration (400 m was chosen because it was the radius of the maximum home range occupied by an individual bird of any sex during any season recorded by Herzog and Boag, 1978). In comparing dates (and distances), median values were used to reduce the statistical influence of outlier points.

Social behaviour in winter was analyzed by examining the composition and stability of flocks. Any association of two or more birds, with a maximum nearest-neighbor distance of 50 m, was considered a flock. Although a maximum nearest-neighbor distance of 18 m was used by Ellison (1973), interindividual awareness in this area (Nugent and Boag 1982) warranted the larger 50 m distance. Grouse observed in the same flock during consecutive sightings (maximum time of 3 days between sightings) were considered part of a stable flock. Because many of the areas adjacent to the Gorge Creek study area consisted of slightly different grouse

Figure 1. Distribution of spring dispersal and migratory distances for radio-tracked female (n = 65) and male (n = 28) spruce grouse in southwestern Alberta.



densities and habitat types, I analyzed only flocking data obtained on the main study area.

RESULTS

Distances of movement

Females were recorded moving up to about 11 km during the spring phase of dispersal and migration, and males up to 10 km (Fig. 1). The relative number of birds moving > 2 km during spring dispersal did not differ from that migrating, either for males or females ($P >$ 0.50; Chi-square contingency table). The similarity between the distances moved during the spring phase of dispersal and migration for each sex is expected if the latter merely retraces a bird's first spring dispersal movement. An examination of fidelity of females to a winter range showed that of 30 birds (15 short-distance and 15 long-distance migrants) observed during their first winter as juveniles/yearlings and again in subsequent winter(s) as adults, only one had a winter range as an adult more than 500 m away from its first winter range (950 m). The median distance between successive winter ranges of an individual female was 154 m. Because of the apparent retracing of spring dispersal movements as subsequent migrations, they were combined for comparing male and female movements. Females moved > 2 km significantly more frequently than males ($P < 0.01$; Chi-square contingency table).

Timing of migration

The median dates of migration for females undertaking long or short migrations were not significantly different (Table 1). However, long-distance migrants deviated significantly less from the overall median dates of movement than did short-distance migrants ($P = 0.005$; Klotz test for equal variances).

Some of the variability in the timing of short migrations (< 2 km) appeared to reflect repeated migratory trips during a single season. For example, some females moved to their winter range, returned to summer range, and finally moved back to winter range, all during a

Table 1. Median dates of departure from and arrival on summer and winter ranges for radio-tracked migrating female spruce grouse in southwestern Alberta.

	Short migrations			Long migrations			
Category	N	Median/	Range	N	Median	Range	Overall median
Last sighting on winter range	5	17 Apr.	19 Mar.-8 May	8	26 Apr.	16 Apr.-11 May	25 Apr.
First sighting on summer range	5	19 Apr.	1 Apr.-11 May	7	27 Apr.	23 Apr.-16 May	26 Apr.
Last sighting on summer range	6	11 Oct.[1]	3 Aug.-18 Dec.	6	12 Sep.	30 Aug.-13 Oct.	13 Sep.
First sighting on winter range	9	31 Aug.[1]	19 Jul.-23 Sep.	7	27 Sep.	9 Sep.-16 Oct.	23 Sep.

[1]Because of frequent reverse migratory trips, the last sighting on the summer range is later than the first sighting on the winter range.

single fall season. This type of movement was observed in 15 females during this study. All but one were short-distance migrants. The one exception was a female that moved 2.15 km, only marginally greater than the separation point between long and short migration (2 km). Although repeat migratory trips would probably be more difficult for long-distance migrants to make, because of the longer distances moved, none of the long-distance migrants (apart from the above exception) reversed its direction during a migratory movement, even for a single day.

Winter flocking

Long-distance migrants flocked with other birds significantly more than did short-distance migrants (Table 2). The difference appeared to reflect their association with other adult females as opposed to flocking in general. For example, both categories of migrants flocked equally with birds other than adult females. A more detailed examination of flocks containing more than one female, showed that long-distance and short-distance migrants flocked equally with long-distance migrants (Table 3). However, adult females that were short-distance migrants associated significantly less often with other short-distance migrants than did long-distance migrants.

Similar results were recorded when the composition of stable flocks was examined. Short-distance migrants were less common in stable flocks than expected, based on their frequency of occurrence in the population ($P < 0.05$; Chi-square contingency table). Additionally, stable flocks with two or more long-distance migrants appeared to be more common (7 recorded) than flocks with two or more short-distance migrants (2 recorded). Furthermore, stable flocks with two or more adult females present were of greater duration when composed of long-distance migrants ($x = 6.6$ days) than short-distance migrants ($x = 3.0$ days). This occurred despite the fact that short-distance migrants outnumbered long-distance ones by approximately 2:1 in the Gorge Creek population.

Table 2. Associations among adult female spruce grouse in winter flocks in southwestern Alberta (percent in parentheses).

Category of migrant	Number of female sightings	No. in flocks[1]	No. in flocks with birds other than adult females[2]	No. in flocks with other adult females[2]
Long distance	157	73 (46.5)	44 (28.0)	54 (34.4)
Short distance	419	147 (35.1)	121 (28.9)	45 (10.7)
P[3]		< 0.05	> 0.50	< 0.001

[1]Some flocks contained both adult females and non-adult females.

[2]Categories not exclusive.

[3]Chi-square contingency table.

Table 3. Associations among adult female spruce grouse in winter flocks in southwestern Alberta in relation to their migratory status (pecent in parentheses).

Category of migrant	Number of flocks containing females[1]	No. in flocks containing short-distance migrants[2]	No. in flocks containing long-distance migrants[2]
Long distance	54	31 (57.4)	32 (59.3)
Short distance	45	16 (35.6)	31 (68.9)
P[3]		< 0.05	> 0.10

[1]Some flocks contained both short-distance and long-distance migrants.

[2]Categories not exclusive.

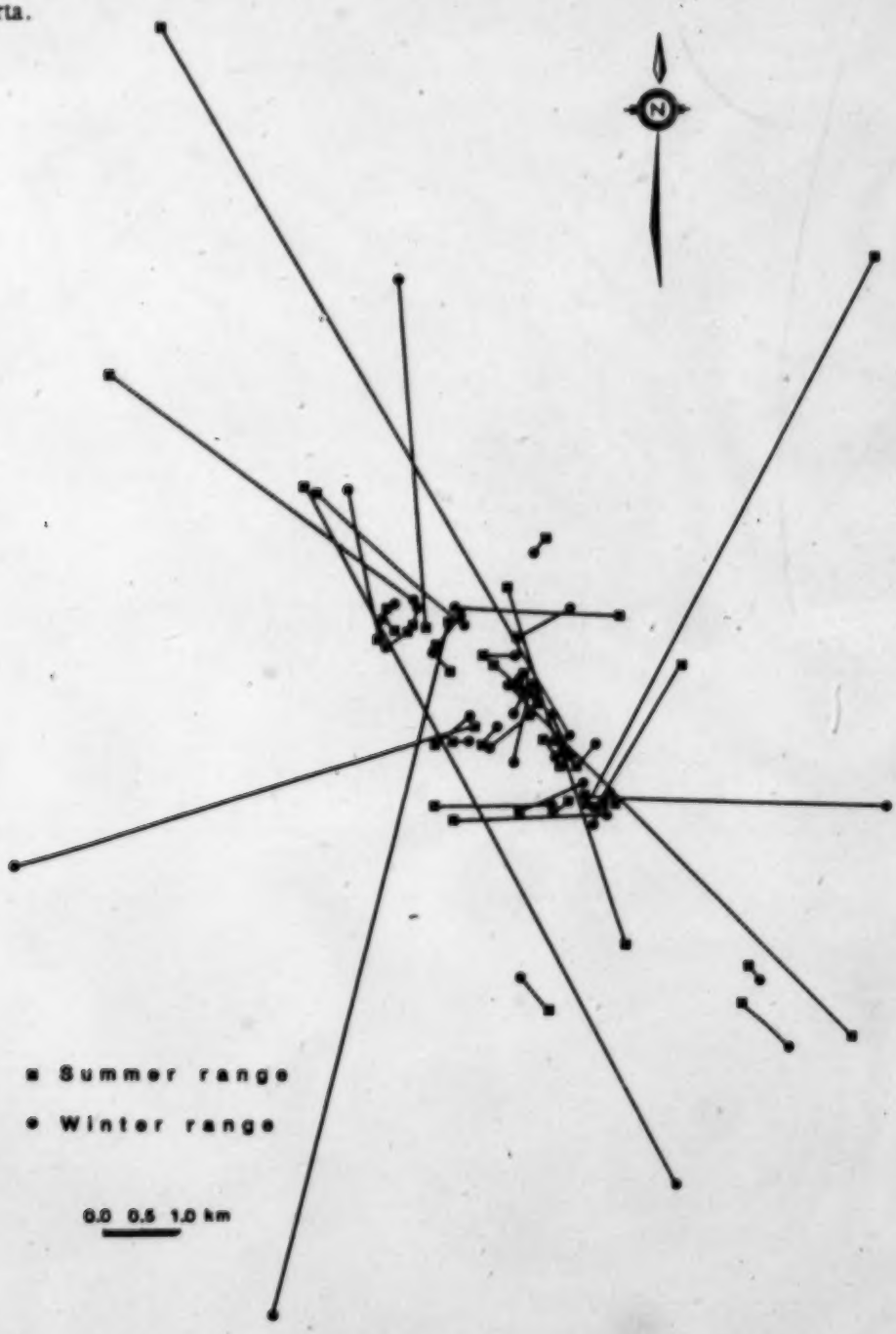
[3]Chi-square contingency table.

DISCUSSION

These results show that distances covered during the spring phase of dispersal and subsequent migration are similar, thus supporting Herzog and Keppie's (1980) suggestion that migration may be a retracing of the preceding movement made during the spring phase of dispersal. This suggestion is also supported by the high degree of site fidelity of birds to their first wintering area, to which they return after making a spring dispersal movement, as well as to their first breeding area (Herzog and Keppie 1980). These observations imply that the spring phase of dispersal is an important event in the life history of individual spruce grouse. Factors that influence how far a yearling will disperse in spring may also influence its subsequent migratory behaviour.

Since most females apparently breed during their first spring, they may be forced to move from winter range to find a vacant territory (Herzog and Boag 1977, 1978, Boag et al. 1979, Nugent and Boag 1982). Differences in the timing of migration may reflect different proximal reasons for the original dispersal movements. For example, intrasexual interactions may be responsible for the movements observed in short-distance migrants, as well as in short-distance dispersers. Since the filling of vacant space occurs over time (Nugent and Boag 1982), such intrasexual interactions could explain the variation in the timing of dispersal and migration in these short-distance migrants. Although this study did not show that there is a direct relationship between aggressive interactions and migration distance, it appeared to indicate that the migratory patterns of short-distance migrants are not as fixed as those of long-distance migrants. It is unlikely, however, that intrasexual interactions would force a bird to move over 5 km in a straight line as is seen in many long-distance migrants/dispersers. Moreover, long-distance migrants are not making this movement in response to the lack of suitable habitat because many birds commonly move through habitats used by others and thus apparently suitable (Fig. 2). Additionally, some spruce grouse spend both the winter and breeding seasons on the same areas (Herzog and Keppie 1980), suggesting that selection of separate habitats in each season is not a major factor evoking long movements. The apparently

Figure 2. Directions and distances of straight-line migratory paths between the median locations of winter and summer ranges for radio-tracked female spruce grouse in southwestern Alberta.



random direction of migratory movements ($P > 0.50$; Chi-square test) also seems to rule out the importance of broad habitat differences in influencing long movements, such as with the seasonal changes in elevation and habitat reported for Blue Grouse (*Dendragapus obscurus*)(Anthony 1903, Marshall 1946, Wing 1947, Bendell 1955, Mussehl 1960, Zwickel et al. 1968).

If some birds are looking for a place to breed during their first winter (Alway and Boag 1979), they may display more spatial separation with respect to other potential breeders; a behaviour similar to the territorial behaviour that grouse display in spring (Herzog and Boag 1977, 1978). If such spatial separation in the winter is important among potential breeders, it should be more prevalent among short-distance dispersers/migrants. Not only did short-distance migrants flock less than long-distance migrants, they also flocked less with other adult female spruce grouse. Additionally, in flocks containing females, short-distance migrants were observed significantly less often with other short-distance migrants than were long-distance migrants. Since both categories of migrants were observed on the same area and in the same general habitat, there is no obvious habitat-related reason why they should differ in their relative flocking tendencies. Furthermore, the median distance moved of 0.33 km for short-distance migrants suggests that they may not be remaining entirely on their summer territories during the winter and hence, they are probably available for flocking with other females. Since the two categories of migrants are essentially equally represented in flocks with non-females, I suggest that short-distance migrants are not avoiding flocking in general, but are avoiding other females, and especially other short-distance migrants. The result of such intrasexual avoidance may be that short-distance migrants are spatially separated in the winter. Additionally, the lack of intrasexual avoidance by long-distance migrants may indicate that they are not immediate competitors for space in which to breed.

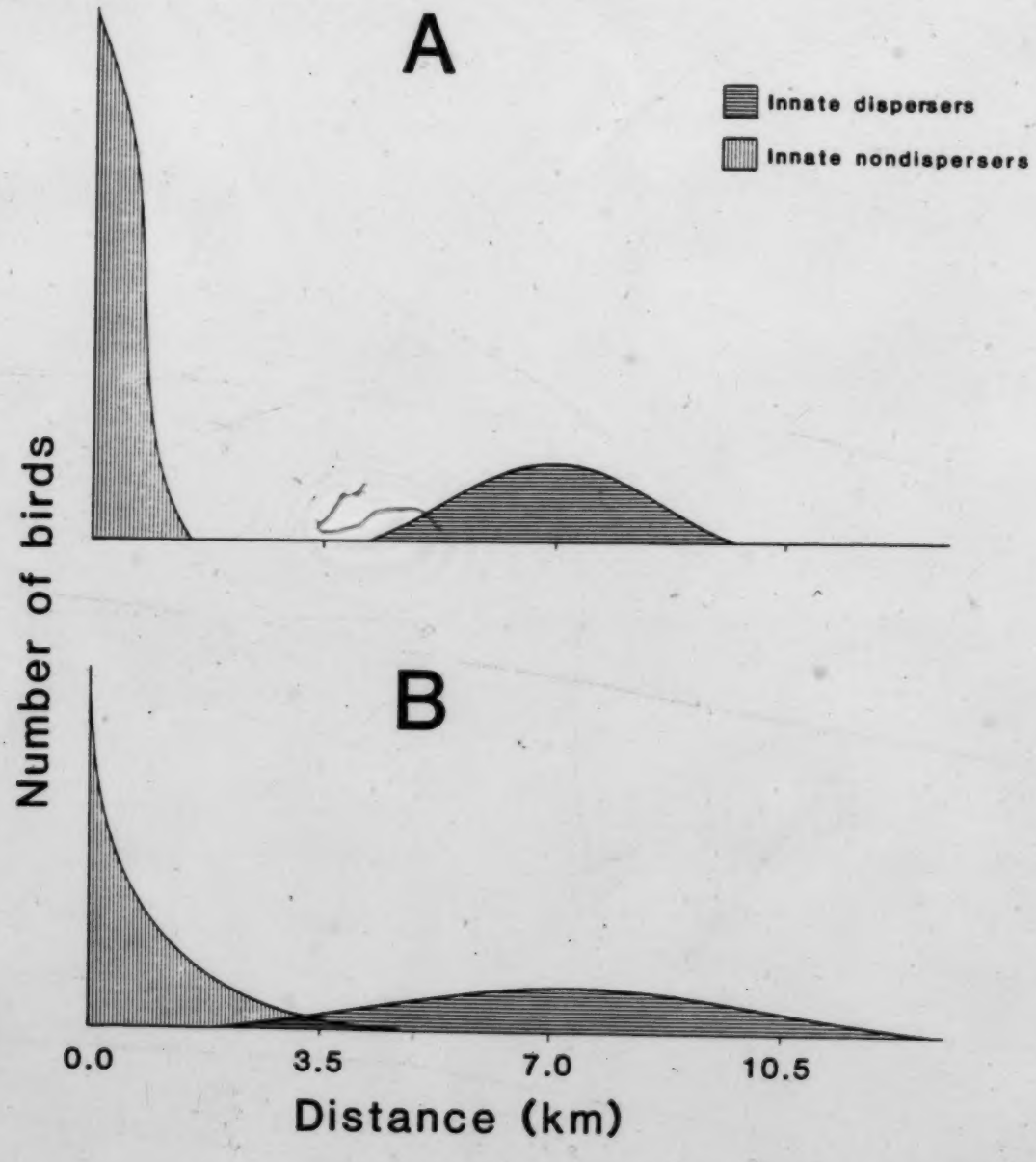
The data on dispersal and migration distances from this study suggests that both males and females are not moving random distances, based on a Poisson distribution ($P < 0.001$; Chi-square test). These results suggest that there is a significant amount of clumping in both

the short and long distance categories. For example, more females are moving either < 1.0 km or > 4.5 km than expected by chance (Poisson distribution based on a mean distance of movement of about 2.0 km).

On a broader scale, both innate and environmental factors (Howard 1960) may work synergistically to modify what may be a bimodal distribution in dispersal and migration distances (Fig. 3). The basic pattern of dispersal in this population may be bimodal (Fig. 3A), but because of population pressures this pattern may be masked (Fig. 3B).

Male spruce grouse may exhibit a pattern similar to females in distances moved during the spring phase of dispersal and migration. Although a small sample size has prevented a detailed examination of these movements, those made by males may be influenced in a manner similar to that for females. Males that do move long distances appear to be in flocks frequently and tend to move very little in the winter, unlike other males. Since non-breeders are more common among yearling males than females (Herzog and Boag 1978), males may be less inclined to disperse in the spring because intrasexual population pressure would be less if a territory is not sought. However, innate movements may be similar to those of females, even if they are less frequent.

Figure 3. Hypothetical distribution of distances moved by spruce grouse during the spring phase of dispersal and migration, based on innate factors alone (A), and with the influence of population pressure superimposed (B).



LITERATURE CITED

ALWAY, J. H., AND D. A. BOAG. 1979. Behaviour of captive spruce grouse at the time broods break up and juveniles disperse. Can. J. Zool. 57:1311-1317.

ANTHONY, A. W. 1903. Migration of Richardson's grouse. Auk 20:24-27.

BENDELL, J. F. 1955. Age, breeding behavior, and migration of sooty grouse, *Dendragapus obscurus fuliginosus* (Ridgway). N. Amer. Wild. Conf. Trans. 20:367-381.

BOAG, D. A., K. H. MCCOURT, P. W. HERZOG, AND J. H. ALWAY. 1979. Population regulation in spruce grouse: a working hypothesis. Can. J. Zool. 57:2275-2284.

ELLISON, L. N. 1973. Seasonal social organization and movements of spruce grouse. Condor 74:375-385.

GAINES, M. S., AND L. R. MCCLENAGHAN. 1980. Dispersal in small mammals. Ann. Rev. Ecol. Syst. 11:163-196.

GREENWOOD, P. J., AND P. H. HARVEY. 1982. Natal and breeding dispersal in birds. Ann. Rev. Ecol. Syst. 13:1-21.

HERZOG, P. W., AND D. A. BOAG. 1977. Seasonal changes in aggressive behavior of female spruce grouse. Can. J. Zool. 55:1734-1739.

HERZOG, P. W., AND D. A. BOAG. 1978. Dispersion and mobility in a local population of spruce grouse. J. Wildl. Manage. 42:853-865.

HERZOG, P. W., AND D. M. KEPPIE. 1980. Migration in a local population of spruce grouse. Condor 82:366-372.

HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Amer. Midl. Nat. 63:152-161.

KEPPIE, D. M. 1975. Dispersal, overwinter mortality, and population size of spruce grouse. Ph.D. diss. Univ. of Alberta, Edmonton.

KEPPIE, D. M. 1979. Dispersal, overwinter mortality, and recruitment of spruce grouse. J. Wildl. Manage. 43:717-727.

MARSHALL, W. H. 1946. Cover preferences, seasonal movements and food habits of Richardson's grouse and ruffed grouse in southern Idaho. Wilson Bull. 58:42-52.

MUSSEHL, T. W. 1960. Blue grouse production, movements and populations in the Bridger Mountains, Montana. J. Wildl. Manage. 24:60-68.

MYERS, J. H., AND C. J. KREBS. 1971. Genetic, behavioral and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecol. Monogr. 41:53-78.

NUGENT, D. P., AND D. A. BOAG. 1982. Communication among territorial female spruce grouse. Can. J. Zool. 60:2624-2632.

SWINGLAND, I. R., AND P. J. GREENWOOD. 1983. The ecology of animal movement. Clarendon Press, Oxford.

WING, L. 1947. Seasonal movements of the blue grouse. N. Amer. Wildl. Conf. Trans. 12:504-509.

ZWICKEL, F. C., AND J. F. BENDELL. 1967. A snare for capturing blue grouse. J. Wildl. Manage. 31:202-204.

ZWICKEL, F. C., I. O. BUSS, AND J. H. BRIGHAM. 1968. Autumn movements of blue grouse and their relevance to populations and management. J. Wildl. Manage. 32:456-468.

CONCLUDING DISCUSSION

Examination of spruce grouse (*Dendragapus canadensis*) broods in the wild has provided new insight into the early development of their behaviour. Interactions were more difficult to observe and follow to their completion in the wild than in captive situations, possibly because of the increased opportunity for mutual avoidance among birds in the wild. Nevertheless, the behaviours associated with interactions were recorded much earlier in the wild than in captivity. Additionally, some behaviours such as the flapping run were found in all ages and seasons in birds studied in the wild, whereas in captivity, the flapping run was considered to be an important behaviour associated with brood break-up and fall dispersal (Alway and Boag 1979). This study has suggested the importance of communication among grouse in the wild and especially among the members of a brood. For example, brood hens appear to respond immediately to the sreep, sury, seer, and purring calls of chicks. The reflexive nature of this response is apparent, because hens appear to respond readily to the chicks of other broods.

The gradually increasing hen-chick and intersibling distances suggest that the cohesion of the brood decreases over the brood period. Whether this reduced cohesion occurs because of reduced dependency of the chicks on the brood hen for brooding and/or protection, or a decrease in responsiveness of the brood hen to the calls of her chicks, or an instinct to disperse and move outward, or an increase in aggressive intersibling interactions, remains to be examined more thoroughly. The results of this study suggest that interindividual distances are increasing throughout the brood period without any overt corresponding increase in agonistic interactions among siblings. Previous work has suggested that agonistic interactions do appear to increase in the fall, but only after the time broods normally would have broken up (Alway 1977).

The timing of brood break-up may influence the fall phase of dispersal in spruce grouse. Almost all brood hens migrate between summer and winter ranges, although the distances of the movements are quite variable. Examination of the timing of both migratory

movement and brood break-up indicates that they overlap considerably. If some juveniles were to experience brood break-up after their brood hen left her summer range on a migratory movement, the movement could substantially affect the distances they move during the fall phase of dispersal. This possibility seems to be supported by observations of intact broods following their migrating mothers. Likewise, the greater fall dispersal distances of females than males may reflect their later date of brood break-up, and thus an increased probability of moving with their migrating mothers over substantial distances.

The existence of areas where spruce grouse concentrate in winter, may also be an important factor influencing the movement of juveniles in the fall. If juveniles were to concentrate in wintering areas, as these results suggest, the actual fall movements of individual juveniles, after they have separated from their brood hen, may involve only their movement to the nearest wintering area.

The similarity between the distance moved during the spring phase of dispersal and subsequent migrations, and the high degree of site fidelity of birds to their first summer (Herzog and Keppie 1980) and winter areas, supports Herzog and Keppie's suggestion that migrations retrace a bird's dispersal movement made during its first spring. Why do some birds disperse long distances in the spring while others move very little? Females were chosen to examine this question in greater detail because a larger percentage of them disperse/migrate long distances. Females that migrated short distances appeared to be avoiding other females and especially other short-distance migrant females in winter flocks. Additionally, short-distance migrants were more variable in the timing of their movements than were long-distance migrants. These behavioural differences may reflect important differences associated with their original spring dispersal. The avoidance by short-distance migrants of other females of the same type would be expected if they originally selected a wintering area where they could potentially remain to breed the following spring.

To obtain a thorough understanding of the ultimate consequences and/or the evolutionary strategies of dispersal, such as the increase of gene flow (Howard 1960, Johnston

1961, Murray 1967), the colonization of suitable habitats (Dice 1952), and the regulation of population size (Errington 1956, Lidicker 1962, French *et al.* 1968, Christian 1970, Myers and Krebs 1971), it is important to examine the proximal factors influencing such dispersal movements. However, studies typically examine dispersal by looking at it as one movement, from the place of birth or hatch to the place of breeding or attempted breeding (Howard 1960). These results suggest that the proximal factors influencing the overall dispersal movements of individuals, at least in spruce grouse, may be many and complex.

LITERATURE CITED

ALWAY, J. H. 1977. A study of social behavior relating to brood break-up and dispersal in Franklin's grouse under captive conditions. M.S. Thesis. Univ. of Alberta, Edmonton. 107p.

ALWAY, J. H., AND D. A. BOAG. 1979. Behaviour of captive spruce grouse at the time broods break up and juveniles disperse. Can. J. Zool. 57:1311-1317.

CHRISTIAN, J. J. 1970. Social subordination, population density, and mammalian evolution. Sci. 168:84-90.

DICE, L. R. 1952. Natural communities. Univ. Michigan Press. Ann Arbor. 547p.

ERRINGTON, P. L. 1956. Factors limiting vertebrate populations. Sci. 124:304-307.

FRENCH, N. R., R. Y. TAGAMI, AND P. HAYDEN. 1968. Dispersal in a population of desert rodents. J. Mammal. 49:272-280.

HERZOG, P. W., AND D. M. KEPPIE. 1980. Migration in a local population of spruce grouse. Condor 82:366-372.

HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Amer. Midl. Nat. 63:152-161.

JOHNSTON, R. F. 1961. Population movements of birds. Condor 63:386-389.

LIDICKER, W. Z. 1962. Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. Amer. Nat. 96:29-33.

MURRAY, B. J., JR. 1967. Dispersal in vertebrates. Ecology 48:975-978.

MYERS, J. H., AND C. J. KREBS. 1971. Genetic, behavioral and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecol. Monogr. 41:53-78.